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A
TEXT-BOOK
OF
MYCOLOGY

BY
ERNST ATHEARN BESSEY^{ESSEY}
PROFESSOR OF BOTANY, MICHIGAN STATE COLLEGE

WITH ONE HUNDRED THIRTY-NINE ILLUSTRATIONS

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*Dedicated to the memory of two
great teachers*

CHARLES EDWIN BESSEY

and

GEORG KLEBS

During the writing of this book the author met with the most cordial cooperation and assistance from very many persons upon whose time and effort he had not the slightest claim. To list all those who have helped him with bibliographical notes, illustrations, advice and information of various kinds would be to name many prominent botanists from America, Europe, Australia, Africa, and Asia. To all these the author tenders his deepest gratitude, and acknowledges that much that may be of value in this book comes from them. Especially does he thank those who gave him photographs or permission to use their published illustrations. To Assistant Professor Forrest C. Strong, a colleague of the author's, acknowledgment must be made of his assistance in preparing the illustrations, both as original photographs and as photographic reproductions of published figures, and to my wife for her invaluable assistance in reading proof and for her encouragement during the progress of the work.

ERNST A. BESSEY.

MICHIGAN STATE COLLEGE,
EAST LANSING, MICHIGAN.

CONTENTS

	PAGE
PREFACE.	V

CHAPTER I

INTRODUCTION	
Fungi, definition	
structure.	
physiology.	
parasitism.	
reproduction.	
History of Mycology	I
Literature Cited	I

CHAPTER II

THE NON-FILAMENTOUS FUNGI.	2
Mycetozoa.	2
Acrasiales	2
Labyrinthulales.	3
Plasmodiophorales	3
Chytridiales	3
Olpidiaceae	3
Woroninaceae	3
Synchytriaceae.	3
Rhizidiaceae.	4
Cladochytriaceae.	4
Literature Cited	5

CHAPTER III

FILAMENTOUS FUNGI: PHYCOMYCETAE	5
Monoblepharidales	6
Blastocladiaceae	6
Monoblepharidaceae	6
Hyphochytriaceae.	6
Saprolegniales	6
Saprolegniaceae.	6
Leptomitaceae	7
Ancylistidaceae.	7
Literature Cited	7

CHAPTER IV

	PAGE
PHYCOMYCETAE: PERONOSPORALES.	82
Pythiaceae.	83
Albuginaceae.	89
Peronosporaceae	91
Literature Cited	96

CHAPTER V

PHYCOMYCETAE: SUB-CLASS ZYGOMYCETAE.	100
Mucorales	100
Mucoraceae	109
Pilobolaceae	109
Piptocephalidaceae	110
Thamnidaceae.	111
Chaetocladiaceae.	111
Choanephoraceae.	111
Mortierellaceae.	112
Endogonaceae	113
Entomophthorales	114
Protomycetales.	119
Literature Cited	121

CHAPTER VI

THE HIGHER FUNGI: CARPOMYCETAE	124
Literature Cited	130

CHAPTER VII

CLASS ASCOMYCETAE: LABOULBENIALES AND DISCOMYCETES	132
Laboulbeniales	141
Lecanorales	145
Pezizales.	152
Operculatae	157
Pezizaceae.	157
Elvelaceae.	158
Inoperculatae	159
Helotiaceae	161
Mollisiaceae	162
Phacidiaceae.	163
Geoglossaceae	165
Cytteriaceae.	166
Tuberales	166
Hysteriales.	169
Hysteriaceae.	170
Taphrinales	170
Ascocorticaceae	172
Taphrinaceae.	173
Literature Cited	173

CHAPTER VIII

	PAGE
ASCOMYCETAE: THE "PYRENO MYCETES"	179
Sphaeriales	180
Fimetiariaceae	189
Chaetomiaceae	189
Melanosporaceae	189
Sphaeriaceae	190
Ceratostomataceae	190
Cucurbitariaceae	191
Amphisphaeriaceae	192
Lophiostomataceae	192
Mycosphaerellaceae	193
Pleosporaceae	194
Gnomoniaceae	195
Allantosphaeriaceae	197
Diaporthaceae	197
Xylariaceae	198
Pyrenulales	198
Hypocreales	199
Hypocreaceae	201
Nectriaceae	201
Clavicipitaceae	202
Dothideales	203
Dothideaceae	203
Phyllachoraceae	203
Hemisphaeriales	206
Stigmatiaceae	207
Polystromellaceae	207
Microthyriaceae	207
Trichopeltaceae	207
Hemisphaeriaceae	207
Pseudosphaeriales	208
Pseudosphaeriaceae	210
Myriangiales	211
Literature Cited	213

CHAPTER IX

ASCOMYCETAE: ERYSIPIHALES, ASPERGILLALES, SACCHAROMYCETALES	210
Erysiphales	218
Erysiphaceae	219
Meliolaceae	224
Englerulaceae	227
Capnodiaceae	227
Trichothyriaceae	228
Aspergillales	228
Aspergillaceae	228

	PAGE
Gymnoascaceae	234
Elaphomycetaceae	234
Onygenaceae	235
Saccharomycetales	235
Endomycetaceae	236
Saccharomycetaceae	237
Ascoideaceae	239
Summary of Class Ascomyceteae	245
Literature Cited	247

CHAPTER X

TELIOSPOREAE: RUSTS AND SMUTS.	251
Uredinales.	254
Melampsoraceae	273
Pucciniaceae	275
Ustilaginales.	277
Ustilaginaceae	279
Tilletiaceae	283
Literature Cited	287

CHAPTER XI

BASIDIOMYCETAE: INTRODUCTION AND HETEROBASIDIAL ORDERS	294
Auriculariales	310
Auriculariaceae	312
Tremellales	313
Tremellaceae	315
Hyaloriaceae	315
Dacryomycetales	316
Dacryomycetaceae	317
Literature Cited	319

CHAPTER XII

BASIDIOMYCETAE: AGARICALES	323
Thelephoraceae	325
Exobasidiaceae	327
Clavariaceae	328
Hydnaceae	329
Polyporaceae	332
Boletaceae	341
Fistulinaceae	342
Agaricaceae	343
Literature Cited	353

CHAPTER XIII

BASIDIOMYCETAE: GASTEROMYCETAE	356
Hymenogastres	358
Rhizopogonaceae	360

the case of *Ceratomyces crassus* (*Boletus edulis*) which is reported by Mez as able to kill a rabbit in a dose of less than one milligram. Some of the fungus poisons are of the nature of toxalbumins.

The whole field of the physiology, just touched upon at a very few points in the foregoing paragraphs, is so vast that most of the problems have not even been mentioned. The relations of oxygen supply, temperature, kind of food, reaction of the medium, etc. to the germination of the spores, to the growth of the mycelium, to the metabolic products of the fungus, to its parasitic activity and to reproduction are almost as various as the organisms themselves. Some fungi show very narrow limitations as regards some of these factors but others are able to grow under the most variable conditions.

The majority of the known species of fungi (aside from the Fungi Imperfecti) have both sexual and asexual reproduction. Klebs studied the physiological relations of both types of reproduction in a few fungi and his findings have been shown by his followers to be true of many other fungi in entirely different groups. A rapidly growing fungus of the Saprolegniaceae when transferred to water with low mineral content (e.g. distilled water) quickly develops its asexual reproductive organs, the zoosporangia, and produces an abundance of zoospores. A medium rich in food, especially protein food, is not favorable for reproduction but may favor excessive vegetative growth. As the food supply of the medium is exhausted or if the mycelium is transferred to a medium where the supply of food is less, sexual reproduction may be induced. Thus Miss Kanouse was able to induce production of oogones in *Saprolegnia parasitica* by transferring a bit of mycelium to distilled water with one or two entire hemp seeds with seed coat unbroken. The nutrients diffuse very slowly out of such a seed and the conditions are favorable for oogone formation, which is otherwise almost impossible to obtain with this species.

Sexual reproduction is so extremely different in its details in the various groups of fungi that only a few general points may be mentioned in this introductory chapter, leaving the more detailed discussions to the various chapters in which the organisms are described. The uniting cells may be the entire unicellular organisms in such dissimilar and totally unrelated groups as *Olpidiopsis* among the Chytridiales and *Zygaccharomyces* in the Saccharomycetales.

More often special sexual cells, the gametes, are produced. These may be motile and equal, e.g. in *Olpidium* or *Synchytrium*, or motile and unequal, as in *Allomyces*, or the female gametes (eggs) may be larger and non-motile while the male gametes (sperms) are small and motile, seeking out the eggs and fertilizing them, as in *Monoblepharis*. In some of the Ascomyceteae the male gamete is set free as a naked or very thin-walled, non-motile sperm which becomes attached to the oogone or to an extension of it, the trichogyne, the male nucleus entering through an opening dissolved in the wall and eventually reaching the egg nucleus. In most of the Saprolegniales and Peronosporales separate sperm cells are not produced but the sperm nuclei are introduced into the oogone through an opening and there find the egg nuclei. Whole multi-nucleate gametangia distinguishable or non-distinguishable as to sex may fuse, the nuclei from the two gametangia pairing off and eventually uniting (many Mucorales, *Albugo* in Peronosporales, etc.). In some of the Ustilaginales, Uredinales and Basidiomyceteae any cell of a plant of one sexual phase may unite with any cell of a plant of the opposite phase, even though in the Rusts (Uredinales) there are also special male gametes and special female receptive hyphae.

The product of the sexual union may be a single cell (zygospore or oospore respectively if the uniting gametes are equal or unequal) or a complex of cells (spore-fruit) some cells of which become the reproductive spores (e.g. an apothecium producing as its reproductive spores the ascospores). The complexity of the spore-fruit may be very great. Alternation of generations may occur in some cases (e.g. Uredinales).

In most fungi meiosis (reduction division) occurs very shortly after the sexual fusion so that a phase of growth containing diploid nuclei is very short or entirely lacking. Many fungi, however, show a pairing of nuclei, without uniting, which persists for a long while throughout the active growth of the mycelium which thus has binucleate cells (dicaryon phase), union of the nuclei occurring only in special cells (teliospores, basidia, asci), to be followed immediately by meiosis.

Throughout almost the whole range, from the lowest to the highest fungi, parthenogenesis appears at many points. In the Saprolegniaceae oospores develop without fertilization in many species, and in some of the Mucorales and Entomophthorales we find

PREFACE

The author's experience, both as a teacher of classes in mycology for twenty-four years, and as a student and teacher of plant pathology, has convinced him that no satisfactory text-book of mycology is available in the English language. Gäumann-Dodges' *Comparative Morphology of Fungi*, while excellent as a reference book and indispensable for advanced students of mycology, is too detailed for use in a first year course in the subject. It is hoped, therefore, that this book will meet the need for a text that shall give to the would-be plant pathologist an idea of the structure, life history and classification of the more important groups of parasitic fungi.

An adequate text-book should contain, in addition to undoubted fungi, forms believed by the author, and others, not to be true fungi, nor even plants (e.g. Mycetozoa, Plasmodiophorales). Since a study of only the parasitic forms leaves the systematic relationships at loose ends, all groups of fungi must be included, otherwise, it would not meet the requirements of those studying the subject, not as plant pathologists, but as mycologically interested botanists.

This book is not a text-book of the physiology of fungi, hence the physiological aspects are subordinated to the morphological, ontogenetical, and systematic features. Some attention is given to the more recent studies upon the sexuality of fungi, as these are of importance from both pathological and mycological standpoints, as well as from the light they throw on the questions of sexuality and genetics in other organisms. One chapter is devoted to the literature for the identification of fungi, and although it is not exhaustive, it will be found to be of considerable value, and reasonably up to date, at the time of going to press.

The author, influenced by the teachings of his father, the late Charles E. Bessey (1845-1915), has always had great interest in phylogenetic speculations, valueless though these are considered to be by some botanists, particularly by those who are firmly wedded to

the system of classification to which they have been long accustomed. He believes that these speculations may stimulate studies in the life-history, cytology, morphology, etc. of various groups of fungi, and thus clear the way for laying the foundations of a more logical system of classification. In deference to the preferences of many, the author has attempted to put the discussions of phylogeny in special portions of each chapter. It is hoped that while the study of the fungi themselves may be the chief object for using the book, yet these suggestions as to phylogeny may arouse a spirit of inquiry in the student and so direct his attention to groups of fungi that a better knowledge of them may serve to bring about a better system than our present imperfect systems of classification.

Because the time available for a first course in mycology varies from twelve weeks to a whole college year in different institutions it will be necessary for some teachers to omit certain chapters and parts of chapters. If a teacher can not do this with wisdom and discretion he should not be teaching mycology. It is assumed that any student attempting to use this book will have had the equivalent of a year's course in general botany, or of, at least, one semester's study of that subject, as mycology is a branch of botany and needs a background of general botany. The "Literature Cited" at the close of each chapter is not intended to be a complete bibliography of the subject matter of that chapter. All books or articles referred to in the text are cited here in as complete and accurate a manner as possible. Only the most easily comprehensible abbreviations are used, as it has been the author's experience as a teacher and investigator for thirty-five years, that abbreviations in citations have been responsible for far too many mistakes. Many have been the hours and even days wasted in tracing down a paper that had been incompletely, or imperfectly cited. Perhaps this experience has led the author to err too much in the other direction.

The illustrations are taken, mostly, from the more recent periodicals and monographs. Very few of the stand-bys of the last fifty years will be found in this book. It has been the aim to illustrate several genera and to give some life-history figures for most of the orders discussed. The original author of each illustration is indicated. If there has been any mistake, it is unintentional.

azygospores. Many of the yeasts (Saccharomycetales) produce parthenogenetic asci. Some species of smuts (*Ustilago*) and of rusts (Uredinales) produce teliospores in which union of nuclei is lacking. Similar phenomena occur in the basidia of some of the Agaricaceae.

Asexual reproduction may consist of (1) the fragmentation of the whole fungus, or of large portions of it; (2) the cutting off of special cells (conidia); (3) the setting free of swimming cells (zoospores) produced in zoosporangia; (4) the release of non-motile aplanospores produced within sporangia. In all the recognized classes of mycelium-producing fungi there are found species in which certain cells or segments of the mycelium become enlarged, thick-walled, and filled with food. Such cells may be terminal or intercalary, single or two or more together. These cells are called chlamydospores and are able to survive under conditions unfavorable to the growth or maintenance of the mycelium or of the usual reproductive cells. Upon the recurrence of favorable conditions the chlamydospores germinate. The application of this name to cells in which the sexual union of nuclei occurs, as in the Ustilaginales, is entirely erroneous.

Some fungi produce dense, hard masses of hyphae whose cells adhere and become more or less polyhedral by mutual pressure. These cells become filled with food. Such a structure is a sclerotium (plural, sclerotia). They may have a firm external layer, often dark in color, or this layer may not be much different from the underlying cells. In *Sclerotium rolfsii*, and some other species, the sclerotia are small and adapted for distribution by surface water during heavy rains. In general, however, the sclerotia, like the chlamydospores, are merely organs to permit the survival of the fungus during unfavorable conditions. In some cases they are the only known means of reproduction. In other cases they give rise themselves to the typical reproductive organs, e.g. sclerotia of *Claviceps*, *Sclerotinia*, some species of *Polyporus*, etc.

A number of fungi produce long strands of closely packed hyphae, with a more or less firm cortical layer, which creep long distances, often through very unfavorable environments, to a new location where the fungus establishes itself. Such rhizomorphs are very characteristic of *Armillaria mellea*, the Honey Mushroom, which attacks the roots of many kinds of trees and whose black, branching

rhizomorphs may often be found underneath the dead bark of the roots or even the trunks.

A very brief sketch of a few steps in the history of mycology should not be omitted. The larger fungi, or rather their conspicuous fruiting bodies, were well known to the ancients, but the knowledge of their true nature and manner of growth had to await the invention of the microscope. The Romans knew and distinguished various edible and poisonous mushrooms. The Emperor Nero is reported to have been very fond of *Amanita caesarea*, which owes its specific name to this association. The word fungus (related to the verb *fungor*, to flourish) was applied to mushrooms and to excrescences from the ground or from trees. The Greek word *mykes* (μύκης) was applied to some types of fungi. From this comes the characteristic part of the word mycology. For untold centuries the Chinese have known and used certain fungi for food and others for medicine but, as with the Occident, with little real knowledge as to the true nature of these organisms.

After the invention of printing in Europe there began to appear various "herbals," describing and, in many cases, illustrating more or less elaborately, the various plants of southern and western Europe. In some of these the larger fungi are illustrated. Thus Clusius (Charles de la Cluse, 1529-1609) in 1601 devoted many illustrations and many pages of text to the discussion of edible and poisonous fungi. No attempt was made to classify these into genera or families as these terms are now used. In 1623 in his *Pinax Theatri Botanici*, Gaspard Bauhin (1560-1624) attempted to bring together all plants known to him or to his predecessors. He divided the approximately 100 species of fungi and lichens into groups to which he gave names. The idea of the genus as a definite category for the purposes of classification had not yet become firmly established, so that some of his group names include directly as the next subordinate rank the species while in other cases there are intermediate categories. All lichens he included in the group *Muscus Saxatilis vel Lichen* (nine species). Under the name *Fungus* he included 81 species distributed now among the Agaricaceae, Boletaceae, Polyporaceae, Clavariaceae, Auriculariaceae, Lycoperdaceae, Phallaceae, Clathraceae, Pezizaceae and perhaps other families. *Agaricum Fungus* corresponds practically to the laterally attached Polyporaceae, especially *Fomes*. *Tubera*, with two spe-

cies, was applied to truffles (*Tuber*) and other subterranean firm fungi.

Tournefort (1656-1708) is the botanist who, more than any other, brought to general acceptance the concept of the genus as the classificatory category next above the species. He still maintained the cumbersome method of naming a species with the genus name followed by a descriptive phrase; now universally abandoned for the binomial manner of writing a name which was introduced by Linnaeus (1707-1778). Six genera of fungi and one of lichens were recognized by Tournefort in his "Elemens de Botanique" in 1694. The generic names used were adopted from his predecessors. *Fungus* corresponds to all centrally stipitate Agaricaceae, Boletaceae and Polyporaceae, *Boletus* includes *Morchella*, *Clathrus* and *Phallus*, *Agaricus* was applied to fungi attached laterally to trees, logs, etc., such as various Polyporaceae, *Auricularia*, etc. *Lycoperdon* included the Lycoperdaceae but also the larger round Mycetozoa. *Coralloides* included various branched fungi, among others the branching species of *Clavaria*. *Tubera* was used as by Bauhin.

Dillenius (1687-1747) added a good many species and some new genera. He also changed the names of some groups from those used by Tournefort or, retaining the name, changed its application. Thus all centrally stipitate Agaricaceae are placed in the genus *Amanita*. *Boletus* is entirely changed and made to include the present Boletaceae and centrally stipitate Polyporaceae. *Morchella* and *Phallus* are introduced to take up the species included in Tournefort's *Boletus*, *Bovista* is substituted for *Lycoperdon* and *Fungoides* for *Coralloides*. For cup or saucer shaped fungi Dillenius uses the name *Peziza*. Mention must be made of Vaillant (Sebastien Vaillant, 1669-1722) whose "Botanicon Parisiense" in 1727 gave illustrations of fungi and other plants whose accuracy and beauty were scarcely equalled for over a century. He listed all genera alphabetically, regardless of their real relationship, hence the fungi are scattered throughout the work. *Agaricus* and *Boletus* are used about as used by Tournefort. Most of the Agaricaceae are included in the genus *Fungus* which is, however, a very heterogeneous assemblage of organisms. *Fungoides* is in part *Peziza* and *Corallofungus* includes some of the species of *Clavaria*. Aside from the beautiful illustrations and the descriptions Vaillant added little to Mycology.

The foremost student of fungi before the time of Linnaeus was the Italian botanist Micheli (Pier Antonio Micheli 1679-1737). He was apparently the first student of these organisms to use the microscope on them, crude as was his instrument. His great work "Nova Plantarum Genera" was completed by 1719 but, for lack of funds, the first part only was published, after a delay of ten years, in 1729. His biographer Targioni-Tozzetti, reports that the second part was completed but never published for lack of means. There is no doubt that Micheli knew his fungi far better than any of his forerunners or contemporaries. He gave usable keys by which genera could be identified and for the larger genera keys to the species. Many of his figures and descriptions were so excellent that there is no difficulty now in identifying the species. He distinguished *Fungi lamellati* (= Agaricaceae), *Fungi porosi* (= Polyporaceae and Boletaceae), *Fungi pulverentes* (= Lycoperdaceae and some others), *Fungi ramosi* (the branching Clavariaceae), etc. Among the generic names used by him and still recognized are *Phallus*, *Clavaria*, *Clathrus*, *Lycoperdon*, *Geaster* and *Tuber*. He used *Agaricum* as did his forerunners for laterally attached *Fomes*, *Trametes*, *Fistulina* and *Stereum*. *Polyporus* was confined to the stipitate polypores; *Suillus* to the present *Boletus* and allies; *Erinaceus* to the stipitate Hyd-naceae; *Fungus* to the stipitate Agaricaceae. *Boletus* as used by him is now known as *Morchella*; his *Puccinia* is now called *Gym-nosporangium*. *Coralloides* was equivalent to the branched species of *Clavaria*, etc. In addition to collecting and studying the larger fungi Micheli was perhaps the first botanist to attempt cultures of molds. He sowed spores of "*Mucor*" (evidently *Rhizopus nigricans*) on pieces of squash at one side and "*Aspergillus*" at the other. Each produced its own kind of fungus. He inoculated two pieces of squash with "*Botrytis*," covering one with a bell jar and leaving the other exposed. The covered piece developed only *Botrytis* while the uncovered piece developed *Mucor* as well, thus showing, as Micheli pointed out, that the spores of these various molds were distributed through the air.

Linnaeus (Carl von Linné, 1707-1778), the "Father of Botany" as he is so often called, advanced the knowledge of fungi little if at all. In his great work *Species Plantarum* (1753) he attempted to bring together all of the known species of plants. His adoption of the two word form of name for species (i.e. generic and specific name

as we call them) marked a very great advance in convenience and simplicity. In his twenty fourth class, "Cryptogamia," the fungi are to be found, chiefly under the heading "Cryptogamia Fungi." A few are among the "Cryptogamia Algae." His treatment of the fungi which he knew mostly only from the study of botanical literature and only superficially at first hand, is far less scientific than that of Micheli or even Dillenius. The lichens were included in the genus *Lichen*, among the algae, as was the genus *Tremella*. This genus includes the alga *Nostoc* as well as the rust *Gymnosporangium*, the Basidiomycete *Auricularia*, several lichens and probably one or more species now included in *Tremella*. All of the Agaricaceae as we know the family were included in the genus *Agaricus* and all the pore fungi in the genus *Boletus*, a change in the usage of these two names from that of Micheli and his predecessors. *Erinaceus* of Micheli and earlier botanists becomes *Hydnum*. *Phallus* is made to include both *Phallus* and *Morchella*, being equivalent to Tournefort's *Boletus*. *Lycoperdon* includes Lycoperdaceae and some Mycetozoa. *Mucor* includes all molds such as Mucorales, Fungi Imperfecti and also Erysiphaceae. Other genera recognized by Linnaeus were *Elvella*, *Peziza*, and *Clavaria*.

The most significant advance in the classification of fungi after Linnaeus is to be found in the works of Christiaan Hendrik Persoon (1755-1837). The number of recognized species had become greatly increased and the great improvements in the microscope made it possible to study the manner by which the spores were borne, so that the major groups as now recognized began to appear.

Probably the greatest contribution to the knowledge of the larger fungi, particularly the "Hymenomycetes" was made by Elias Magnus Fries (1794-1878), whose active mycological work extended over a period of more than half a century (Figure 1). The impetus given to mycology by these great botanists was felt over the whole world and fungi unknown to science were discovered by the thousands.

In the first half of the nineteenth century the smaller Ascomyceteae, especially the Sphaeriales, and the pycnidial Fungi Imperfecti, were mostly described superficially, often being thrown together in the same genus. Little was known of the Rusts, Smuts, molds of all sorts, various Moniliales, Melanconiales, etc. Only when these were studied carefully with the compound microscope did order

begin to arise out of chaos. Of the many workers in that period mention may be made of Corda (August Carl Joseph Corda, 1809-1849) whose "*Icones Fungorum*," a six volume work, published from 1837 to 1854, showed the detailed structure of many of the larger fungi but also threw light on hundreds of the microscopic forms. Soon following this came the beautifully illustrated three volume



FIG. 1.—Elias Magnus Fries, aged about 80 years. (After Killermann, 1927.)

work of the Tulasne brothers, "*Selecta Fungorum Carpologia*," 1861-1865 (Louis René Tulasne, 1815-1885 being the chief author).

As new species of fungi were recognized in all parts of the world their descriptions appeared in all sorts of scientific journals, reports of learned societies, and even in text-books, so that it became increasingly difficult for a student of fungi to know whether a fungus under study by him was new to science or already described. Many fungi were unavoidably named several times by different investigators. In Germany and other European countries floras were published in which were described all species of fungi known to occur in those regions, such, for example, as Rabenhorst's *Kryptogamenflora*. Valuable as were such works, they did not include fungi from other

Their first publications along these lines appeared between 1894 and 1896 but were followed by a host of other eager students in all parts of the world. The correction or confirmation of previously held ideas, particularly with reference to the nature of the sexual act in fungi, thus made possible, has proved to be of the utmost value in determining the relationships of fungi.

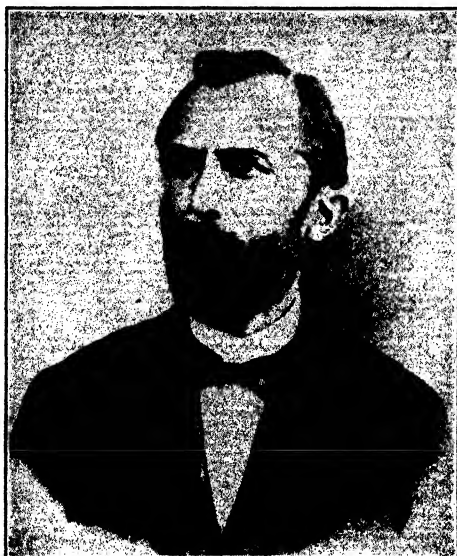


FIG. 3.—Anton de Bary. (After Jost, 1930.)

In 1904 and succeeding years A. F. Blakeslee made known the occurrence of those sexual phenomena in the Mucorales to which he gave the names heterothallism and homothallism. The study of these types of sexual reactions has been extended to other groups of fungi; in the Basidiomyceteae by Mlle. Bensaude, Hans Kniep, Mounce, Vandendries, Hanna, and many others from 1915 to the present; in the Ustilaginales by Bauch, Hanna, Kniep, Stakman and others, in the last 12 or 15 years; in the Uredinales by Craigie, Andrus, Miss Allen, etc. since 1927; in the Ascomyceteae by B. O. Dodge, Ames, Drayton, and several others, mainly since 1927. Dodge, Lindegren and others have made intensive studies on the genetics of fungi in the last few years, particularly in various species

of *Neurospora* while others have studied the smuts from the genetic standpoint. Hybrids have been produced in both these groups as well as in the rusts and their structure and their behavior studied.

The present day finds systematic mycologists active all over the world. Life histories are being studied in all groups, the sexual relations are being scrutinized from the lowest to the highest fungi and genetical studies are revealing results somewhat parallel, but on a vastly smaller scale as yet, to those attained by the study of *Zea mays* and *Drosophila*. As never before is a knowledge of the fungi themselves so necessary.

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be rather primitive but there is a strong possibility that, in some cases at least, simplification from filamentous forms may account for the structure exhibited.

CLASS MYCETOZOA (MYXOMYCETAE)

SLIME MOLDS

The slime molds are chlorophyll-less organisms which are in many cases saprophytic. Other species feed upon bacteria and some

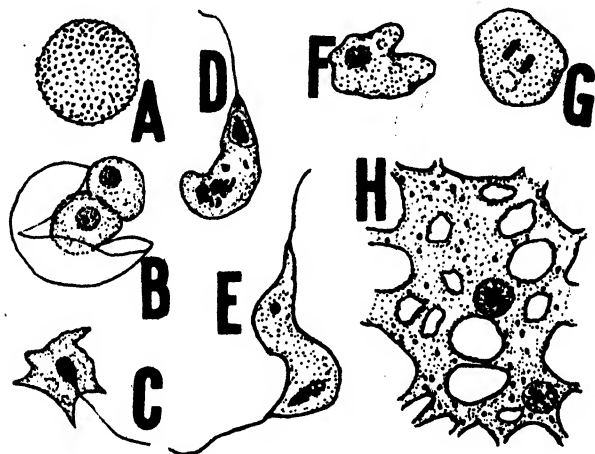


FIG. 4.—Mycetozoa. *Physarum polycephalum*. A, spore; B, germinating spore; C and D, swarm-spores; E, uniting swarm-spores; F and G, amoeboid zygotes; H, portion of plasmodium. (After Howard, 1931.)

digest the hyphae and fruit bodies of higher fungi. According to Lister nearly 300 species are known. These comprise 53 genera, 14 families and three orders. They are world wide in their distribution except for the coldest regions. In brief, their life history is as follows: From the germinating spore there escapes one (sometimes more) amoeboid, naked swarm-spore with a single anterior flagellum. (Gilbert, 1927, describes biflagellate swarm-spores in *Stemonitis fusca*, but as only about one-fourth of the polyhedral cells in such swarmspores and, usually, they are only one color. By the clearly an abnormality.) These motile cells in many cases contain cellulose. They are brown in color. By the action of the *Amoeba* and leave behind the ungerminated spores are permitted to escape. In many cases the ingested food is all the spores escaping from various other objects of an organic nature.

After several divisions, the swarm-spores change their form. The flagellum is retracted, and the cell becomes more rounded, sometimes developing conspicuous pseudopodia. These myxamoebae divide several times. Eventually they begin to unite by twos, with nuclear fusion, to form zygotes. In the genus *Reticularia* Wilson and Cadman have shown that the myxamoebae are not formed but that the sexual union occurs between flagellate swarm-spores. This has also been found to be true for *Didymium difforme* by Miss Cayley and for *Physarum polycephalum* by Howard (Figure 4). Also in *Fuligo*, *Physarum*, *Stemonitis* and other genera Seiji Abe observed the union of the uniflagellate cells produced by the germination of the spores. The cell union was followed by the fusion of the nuclei. The gametes differed in their behavior, one, the male, becoming smaller and being entirely absorbed by the other, to form the amoeboid zygote. The male gamete was found to be negatively and the female gamete positively charged. The zygotes mostly unite with other zygotes without further nuclear union, to form a plasmodium, but single zygotes may grow and become multinucleate plasmodia through division of the zygote nucleus without uniting with other zygotes. The plasmodia are able to ingest and feed upon swarm-spores and myxamoebae. Skupienski claims that in *Didymium difforme* the nuclear fusion does not occur at once upon the union of the myxamoebae. Its growing plasmodium may unite with other plasmodia and myxamoebae, until it becomes large and approaches the time of spore formation. Not until then do the nuclei unite by pairs. Reduction division takes place immediately before sporulation.

The sexual processes described above have been observed in various species of the Sub-class Endosporeae. In the Exosporeae the swarm-spores after several divisions become transformed into myxamoebae which divided further and finally, without any sexual union, fuse into plasmodia, as in the case of *Didymium*.

It creeps through the soil, or in rotten wood, or in organic matter, fruiting bodies of fungi, etc., digesting its food and increasing in size and in the number of zooids. It may emerge as a fine or coarse slimy network over the surface of the substratum (Figure 5, A). This network shows continued creeping motion. The diameter of the zooids may vary from a few milli-

meters up to 15 or 20 centimeters and in color from white to yellow, orange, red, brown, violet and other colors.

Eventually the plasmodium heaps itself up somewhat, on the exterior of its substratum, or even creeps up adjacent objects and there undergoes the changes which lead to the production of the fructifications. These may be separate from one another or may be crowded together into a compound fructification. In the Sub-class Endosporeae there appears externally a non-cellular peridium,



FIG. 5.—Mycetozoa. *Didymium squamulosum*. A, plasmodium; B, fruiting bodies. (After Miss Cayley, 1929.)

secreted by the plasmodium. This may be of various thickness according to the species, and may be encrusted with lime or not. Within the fructification are secreted numerous non-cellular threads and beams which form a sort of framework. This is the capillitium. Its structure and arrangement are of great value in classifying this difficult group of organisms. Between the threads of the capillitium the protoplasm rounds up into innumerable, small, uninucleate cells which secrete cell walls. In *Physarum polycephalum* it has been shown by Howard that the cell walls are secreted before the spores round up, so that at first a continuous mass of polyhedral cells is produced. The cells then begin to round up and the cell walls split. These are the spores. The walls of some species contain cellulose. The spores are most often violet, purple or brown in color. By the rupture or dissolution of the peridium the spores are permitted to escape, the capillitial threads preventing all the spores escaping true
are in this

once. The fructification may be sessile or stalked, round or elongated, scattered or crowded, almost microscopic or, in the case of some of the compound fructifications, up to ten centimeters in length and four to five in width and thickness. In the genus *Ceratiomyxa*, the only genus of the Sub-class Exosporeae, the spores are extruded externally from the fructification instead of being produced inter-

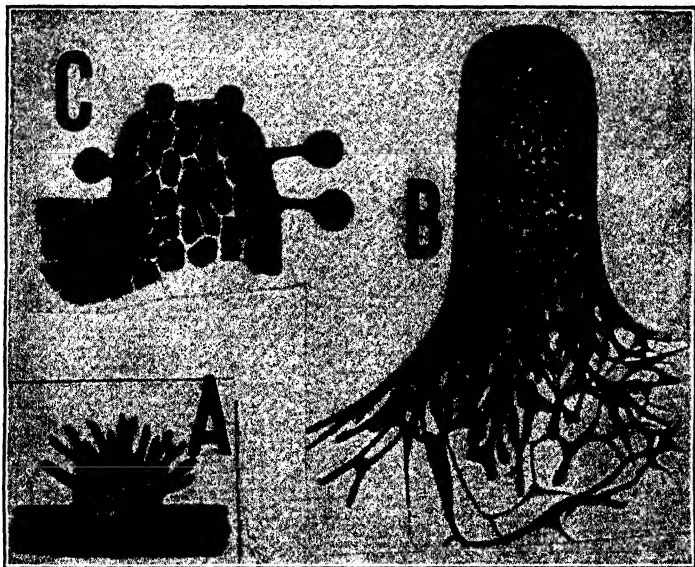


FIG. 6.—Mycetozoa. *Ceratiomyxa fruticulosa*. A, habit sketch; B, development of young fruiting body from plasmodium; C, portion of mature sporophore showing production of external spores. (After Famintzin and Woronin, 1873.)

nally (Figure 6). As the plasmodium creeps out of the wood in which it has been growing it secretes a massive central core of mucilaginous nature on the outside of which the protoplasm creeps as a thin, somewhat reticulate sheet. After a fusion of the numerous nuclei by pairs (according to Olin) the protoplasm undergoes cleavage into uninucleate naked cells each of which sends out a tubular process at the end of which is formed the spore into which the whole protoplasmic contents of the supporting cell pass. The nuclei divide by meiotic division into four nuclei so that the mature spores are quadrinucleate. On germination the nuclei undergo another

division and the protoplasm divides into eight uniflagellate amoeboid swarm-spores.

The point at which reduction division (meiosis) occurs has been demonstrated in several species. This appears to take place in the nuclear divisions immediately preceding spore formation in both Endosporeae and Exosporeae. Where the nuclear union follows immediately upon the union of two myxamoebae or swarm-spores, the plasmodium contains diploid nuclei during its whole existence. In *Didymium* (Endosporeae) and in *Ceratiomyxa* (Exosporeae) the plasmodial nuclei are haploid, inasmuch as the nuclear fusions closely precede the meiotic divisions which give rise to the nuclei of the spores.

The classification of the numerous genera and species is based upon the manner of spore formation (endogenous spores, Sub-class Endosporeae, with two orders and over fifty genera; exogenous spores, Sub-class Exosporeae with one genus), formation of simple or compound fructifications, thickness of the peridium and the presence or absence of lime in it, arrangement of the elements of the capillitium and the microscopic structure of its threads, the color, shape, size and markings of the spores, as well as the characters of the plasmodium, size, color, etc.

Among the endosporous Slime Molds mention should be made of *Stemonitis*, with purple or rust-brown spores, clustered, stalked fruit bodies with the stalk extending upwards as an axial strand (columella) from which branch off the capillitial threads which are combined into a loose network that is surrounded by an evanescent peridium; *Physarum* (Figure 7, C and D) with clustered separate or compacted lime-encrusted fruit bodies and with the capillitial threads expanded here and there and filled with lime granules; *Fuligo*, (Figure 7, A and B) with similar capillitium but with the spore-fruits united into a single large convolute "aethalium," one of the largest slime molds; *Dictydium*, (Figure 7, E) stalked, with no internal capillitium and with the peridium quickly disappearing except for the numerous longitudinal ribs that run from base to apex like the lines of the meridian on a globe; *Arcyria*, with short-stalked fruits, the capillitium lacking a columella and consisting of a network of tubular threads with characteristic thickenings such as spin s, warts, rings, etc..

The fructifications of Slime Molds are their individual plasmodia in contact on rotten plants or stumps, on fungi, on leaves, etc. The Mycetozoa (Figure 8) are true cells. In this

quently on the blades of grass and other vegetation in lawns. Very dry habitats do not favor their occurrence. In moist weather, the plasmodia may be found creeping about on the surface of, or emerging from, the various substrata within which they developed. It is

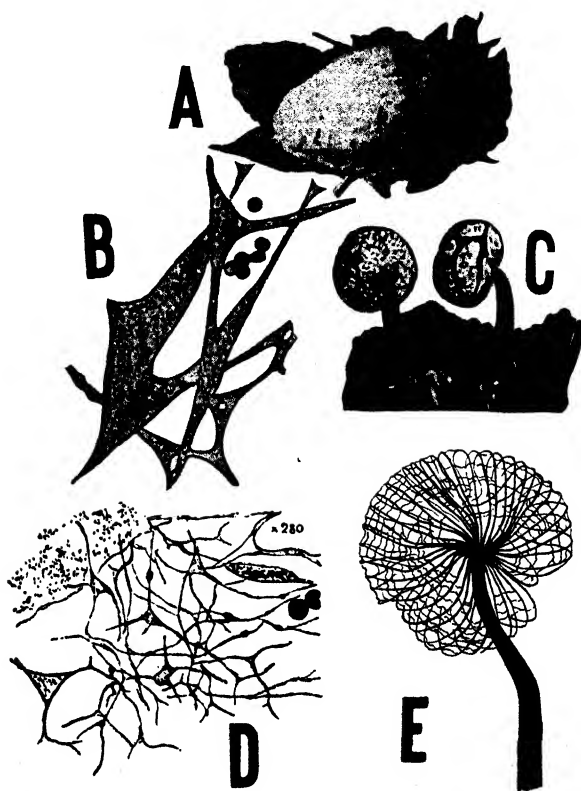


FIG. 7.—Mycetozoa. A, *Fuligo septica*, habit drawing; B, capillitium and spores; C, *Physarum nutans*; D, portion of capillitium; E, *Dictyidium cancellatum*, showing persistent ribs of sporangial wall. (After Lister, 1911.)

possible to grow some species, in pure cultures, from the spores to maturity of the fructification.

Sometimes associated with the Class Mycetozoa are the two orders *Acrasiales* and *Opisthothulales*. Whether they should be included in this class or into two distinct classes the author will not venture to decide. On germination these two orders do the swarm

spores possess flagella although they are amoeboid upon emerging from the spore wall.

The **Acrasiales** (Figure 8) consist of saprophytic organisms, occurring on dung or decaying wood or other organic matter. The spores upon germination give rise to naked amoeboid cells (myxamoebae) with or without conspicuous pseudopodia and containing

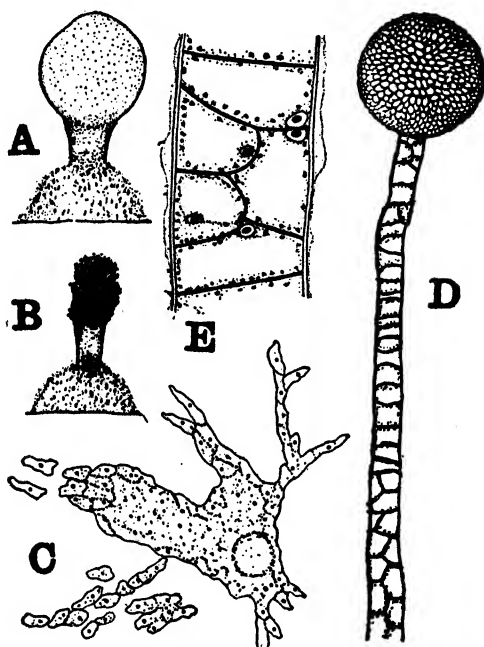


FIG. 8.—Acrasiales. A and B, *Guttulinopsis clavata*; C, pseudoplasmodium of *Polysphondylium violaceum*; D, *Dictyostelium mucoroides*; E, detail of stalk. (After Olive, 1902.)

a single nucleus and one or more food vacuoles. Within these vacuoles are digested the bacteria and other bits of organic matter that serve as food for the organism. These myxamoebae enlarge and divide several times and in *Dictyostelium mucoroides*, according to Skupienski, then unite by twos. The resulting zygotes seem now to be mutually attracted to one another and draw together into heaps of naked cells that maintain their individuality. These heaps of separate cells are called pseudoplasmodia in contrast to the true plasmodia that are found in the Mycetozoa (Figure 8, C). In this

stage, pressure or, in some cases, exposure to bright light will cause the pseudoplasmodium to separate into its individual cells which reassemble again elsewhere. In *Dictyostelium*, Skupienski reports, the cells eventually fuse into a true plasmodium within which the nuclei undergo two more divisions (probably meiotic). In this genus the plasmodium heaps itself up into a conical structure in the basal part of which cellulose walls are produced, separating it into the more or less hexagonal cells of the stalk (Figure 8, *E*) while in the upper, head-like part it breaks up into separate, rounded cells which also develop cellulose walls and become the spores (Figure 8, *D*). These are embedded in a slimy drop. Sexual reproduction and the eventual formation of a true plasmodium have not been reported but probably occur in the other genera of the order. The myxamoebae of *Copromyxa* and *Guttulina* lack conspicuous pseudopodia. The fruiting bodies of the former are sessile, of the latter short stalked. *Dictyostelium*, *Acrasis* and *Polysphondylium* produce myxamoebae with well developed pseudopodia: all produce stalked fruiting bodies (branched in *Polysphondylium*) with ovoid or spherical heads of spores.

The Acrasiales differ from the Mycetozoa in the absence of a flagellate swarm-spore stage preceding the formation of the myxamoebae and in the fact that the naked cells remain distinct for a long time in the pseudoplasmodium forming a true plasmodium only a short time before the fruiting body is produced, if at all. Furthermore no capillitium is formed nor a peridium, although the slime that lies between and around the spores may represent this structure.

The **Labyrinthulales** include parasitic forms, attacking algae, both marine and fresh-water species, and possibly one genus of dung-inhabiting saprophytes. The assembled naked, somewhat amoeboid swarm cells connect themselves, by means of filamentous, terminal, less often lateral, pseudopodial processes into long chains and nets within the host alga. This "net plasmodium" may increase in size through the division of the individual cells. Two means of reproduction are known. The cells round up and become encysted to form spores as in the Acrasiales. From these eventually escape the non-flagellate amoeboid swarm cells. Dangeard has recently described another mode of reproduction. The net plasmodium gradually contracts around the remains of the disintegrated chloro-

plasts and associated cytoplasm of the host cell until the fungus cells come into contact, flattening against each other and forming a hollow sphere in whose center is the granular debris of the host plastids. Within each cell forming this hollow sphere the cytoplasm divides to form four to eight naked swarm cells which escape, as the membrane of the enclosing sporangium disappears. These cells are capable of entering the host cells through minute holes that they dissolve in the cell wall. There they unite into new chains or net plasmodia. Dangeard suggests that a sexual process may occur somewhere in the life history but he did not observe it.

Order Plasmodiophorales.—The relatively few known species that constitute the only family (FAMILY PLASMIDIOPHORACEAE) in this order are sometimes included in the following order (Chytridiales) but in the author's opinion show closer affinity to the Class Mycetozoa in which they are sometimes included. The species in this order are all parasites in the higher (vascular) plants, usually in their roots or in underground (rarely above-ground) portions of their stems; frequently, they cause the formation of swellings or galls on the affected parts of the host plants. The swarm-spores, as in the Mycetozoa, are provided with a single, anterior flagellum. In most cases two swarm-spores unite into an amoeboid zygote which settles on the exterior of the host and dissolves a hole through the epidermal wall, entering the host cell as a naked mass of protoplasm. There by growth and nuclear division is formed a multinucleate naked body (frequently spoken of as a plasmodium) which may break up into several similar bodies. These may, according to some authors, pierce the host cell walls and enter other cells and may be further distributed among various host cells by the division of the latter. The plasmodia enlarge, the nuclear divisions being simultaneous in the same plasmodium. Eventually the nuclei divide twice (meiosis) and the plasmodium divides up into numerous spores which produce cell walls and remain separate or adhere in characteristic forms. Upon the disintegration of the host tissues these spores escape and on germination produce new swarm-cells, one to a spore. Eight such swarm-cells have been reported in *Spongospora*, but Cook denies the correctness of this report.

The life history of *Plasmodiophora brassicae* may well illustrate the main features of the order (Figure 9). The germinating spore (Figure 10, B) produces a naked amoeboid swarm-spore with a

single anterior flagellum. Upon reaching a root hair of cabbage or related plant (mostly the genus *Brassica* and closely related genera in the Family Brassicaceae) the swarm-spore dissolves its way through the host cell wall and enters the cell, the flagellum disappearing before this event. Within the host cell the naked parasite enlarges rapidly and becomes multinucleate (Figure 10, C). This multinuclear structure divides into uninucleate gametangia within

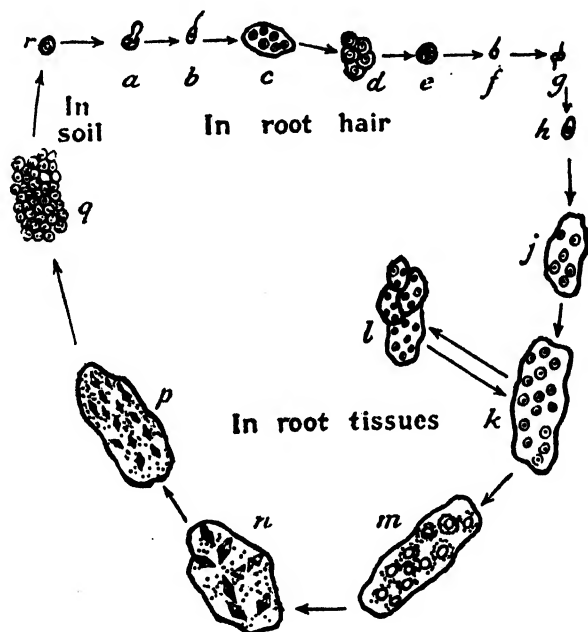


FIG. 9.—Plasmodiophorales. Life cycle of *Plasmodiophora brassicae*. (After Cook and Schwartz, 1930.)

which are formed four to eight apically uniflagellate gametes. These escape and unite by twos or migrate up the root hair into the cortical cells where they unite. The resultant zygotes are rather sluggish amoeboid cells, forming blunt pseudopodia. They are capable of penetrating the host cell walls and thus are enabled to pass from cell to cell. Eventually they lose their power of amoeboid movement and become multinuclear plasmodia (Figure 10, D). In this stage they are unable to enter new cells except as the division of the host cell may distribute them further. Remaining naked, these protoplasmic masses increase in size until they nearly fill the host

cells whose protoplasm is practically destroyed. Then the nuclei undergo two divisions which are believed to be meiotic in nature and the organism divides into naked uninucleate cells which round up and secrete cell walls. These spores are dark in color, smooth and free from one another, nearly filling the host cell (Figure 10, *E*).

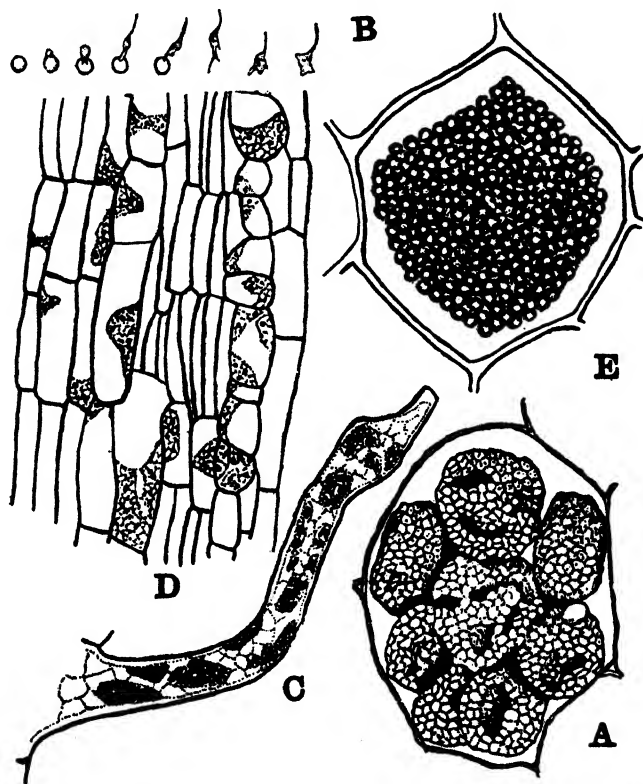


FIG. 10.—Plasmidiophorales. A, spore ball of *Spongospora subterranea*; B–E, *Plasmodiophora brassicae*. B, germination of spores; C, amoebae in root hair; D, plasmodia in root cortex; E, host cell filled with spores. (A after Melhus, 1914; B after Woronin, 1878; C–E after Chupp, 1917.)

von Wettstein reports that the cell walls contain chitin. The infected portion of the host plant under the stimulus of the usually numerous infections undergoes hyperplastic division as well as hypertrophy of the cells so that the roots become much enlarged and somewhat club-like, hence the name "club-root" or "finger^{do.} toes," applied to the disease. The description of the seeds^{w. 921.}

of gametes within the cells of the host is based upon the work of Cook and Schwartz. In a recent contribution, whose accuracy has been questioned by some mycologists, P. M. Jones reports that the spores themselves when germinated in culture do not produce directly an asexual swarm spore but that their contents fragment into numerous minute unflagellate gametes which fuse by twos and produce zygotes. These may either penetrate the root tissues directly or may unite with other zygotes into small plasmodia which then infect the plant. Possibly both accounts are substantially correct, depending upon the condition to which the organism is exposed. This brings the sexual process in this species into agreement with that found in some of the Mycetozoa.

Of the six genera recognized by Dr. W. R. Ivimey Cook in his recent monograph of the order *Plasmodiophora* and *Ligniera* are the only ones whose spores remain separate in the host cells. In *Spongospora subterranea*, the cause of powdery scab of potato tubers, the spores occur grouped together in spore-balls somewhat resembling a sponge (Figure 10, A). In *Sorosphaera* the mass of spores forms a hollow sphere, in *Sorodiscus* the spores are appressed in a two-layered "spore-cake," as if the hollow sphere of *Sorosphaera* had been pressed flat. The spore balls in both genera are surrounded by a common membrane which is reported to be lacking in the other genera. In *Tetramyxa* the spores are formed in groups of four. In these three genera the swarm-cells formed by the germination of the spores unite directly into motile zygotes before infecting the host tissues. In *Ligniera* the spores are free as in *Plasmodiophora*, and upon germination infect the host and give rise directly to a plasmodium. The plasmodium may produce spores or may divide into a number of gametangia within each of which are produced about eight gametes which unite in pairs. The zygotes infect the host and produce plasmodia. Hypertrophy of the host tissue is not known for either of the two recognized species of this genus. In all cases the spores escape only upon the decay or rupture of the containing host cells. Palm and Burk question the validity of the generic segregations within this group, pointing out that a species "*Sorosphaera*" occurring in *Veronica americana*, may in different parts of the host under various conditions produce spore balls like those of *Sorosphaera*, *Sorodiscus*, *Ligniera*, etc. They even suggest host protoplasm.

that perhaps all the species of the order may eventually be placed in but one genus, *Plasmodiophora*.

In common with the Mycetozoa the species of the Order Plasmodiophorales produce amoeboid swarm cells with a single anterior flagellum, show sexual fusion of swarm-spores or of special gametes, and eventually form a naked plasmodium, in which meiotic divisions of the nuclei precede spore formation, and the division of the plasmodium into spores which build cell walls. Neither peridium nor capillitium is produced in the Plasmodiophorales.

The author believes that the Mycetozoa and Plasmodiophorales have arisen close together from the same group of organisms from which the Rhizopoda arose. The Labyrinthulales, in the light of Dangeard's discoveries probably are not far removed. The Acrasiales also, in view of their life history as worked out by Skupienski must be placed close to the Mycetozoa.

Order Chytridiales.—The five or more families included in this order are probably not all closely (if at all) related. Indeed the group may be polyphyletic. Until, however, the life histories of more genera are fully worked out the group may be treated as a unit. The Ancylistidaceae are here excluded from this order since they possess a definite mycelium and are closely related to the filamentous fungi, either as primitive forms or possibly as derived from the filamentous forms by simplification. Whether the Cladochytriaceae should be treated as a further developed group of organisms without true mycelium, but related to the Rhizidiaceae, or whether they represent forms with true but much reduced mycelium must await further studies on the cytology and life history of the fungi found in the family. They are, with some misgivings, included in the Chytridiales. With the Ancylistidaceae excluded the Order Chytridiales consists of about 200 species of mostly parasitic one-celled organisms with apparently the following life history. The naked swarm spore penetrates the host cell directly, or encysts externally and enters the host cell leaving the empty cyst wall on the outside, or remains external except for rhizoids which penetrate the cells. The cell early produces its own cell wall (as of the Mycetozoa, Acrasiales, Labyrinthulales, and Plasmodiophorales which remain naked). The whole cell becomes multinucleated, fragments internally into zoospores or motile gametes (male cells which produce internally zoospores or gametes. Tum as w^{921.})

cells are unflagellate (except Family Woroninaceae in which they are biflagellate) with *posterior* flagellum (not *anterior* as in Mycetozoa and Plasmodiophorales). They either infect the host directly or pair to form a zygote which enters the host and there forms a thick-walled resting spore which later forms swarm-cells. In some cases two cells of the organism that have already penetrated into the host unite to form a resting cell instead of the union taking place between swarm-cells outside of the host.

The Chytridiales are parasitic or less often saprophytic, on algae or small aquatic animals or on the roots, stems and leaves of higher plants. Pollen grains and other types of spores that have fallen into the water are frequently attacked. These fungi are found in the soil or in water. Although most often thought of as freshwater organisms, Petersen reported marine forms nearly thirty years ago and recently Sparrow has restudied these forms and a number of other marine species, parasitic upon Florideae and other algae.

FAMILY OLPIDIACEAE.—The unflagellate swarm-spore with posterior flagellum encysts on the outside of the host cell. A hole is dissolved through the cell wall and the contents of the encysted spore slip into the host cell leaving the empty cyst outside. Once inside, the parasite may swim about actively for a time but it eventually becomes quiescent and enlarges and soon secretes a wall again. Growth and nuclear division occur and soon the whole contents cleave to form swarm-spores which escape through a neck to the outside of the host cell. Sexual reproduction occurs in some genera by the fusing of adjacent cells of the parasite within the same host cell and in other genera by the union of two swarm-spores. In either case a thick-walled zygote results. Eventually this divides internally into swarm-spores. Eight genera are recognized by Fitzpatrick.

The type genus of the family is *Olpidium* of which *O. brassicae* is parasitic in the roots of cabbage and related plants. In this species the swarm-spores may penetrate to even the second or third layer of cells beneath the epidermis. From one to four zoospores may be found within one host cell. If the infection was of the swarm-spore directly, the cell produced is thin-walled and produces swarm-spores in its turn which escape through a length depends upon the cell layer within which the protoplasm. If sexual union of swarm-spores occurred previous

to infection the cell of the parasite is thick-walled and somewhat angular. This zygote is a resting spore and usually does not form its swarm-spores until the following season when they escape through an exit tube. It is probable that all the swarm-spores are always

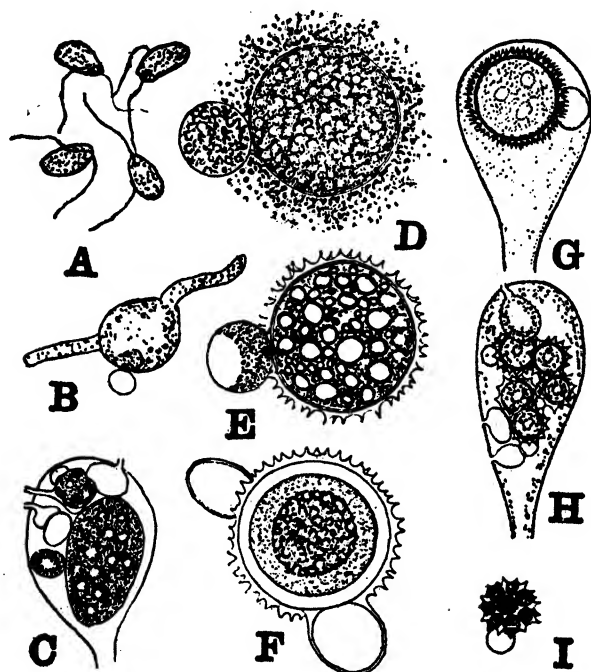


FIG. 11.—Chytridiales, Woroninaceae. A-F, *Olpidiopsis luxurians*. A, zoospores; B, zoospore infecting host; C, young zoosporangium in host; discharged and undischarged sporangia; D and E, successive stages of fertilization of oogone by antherid at an interval of two hours; F, mature oospore with two empty antherids; G, *O. saprolegniae*; H and I, *O. minor*. (A-F after Barrett, 1912, G-I after Sparrow, 1932.)

potential gametes if opportunity for sexual fusion offers or the environment is right, otherwise they function asexually as zoospores. Sexuality has also been observed in *O. viciae* by Kusano. The genus *Pseudolpidiopsis*, occurring in vegetative cells or zygospores of Zygnemataceae, resembles *Olpidium* closely. Sexual reproduction is by the fusion of the adjacent parasites within the host cell, resulting in a thick-walled zygote to which the empty male cell remains attached. Most of the other species of *Olpidium* as w²¹¹

as of the other genera of the family are parasitic in Protozoa, algae or filamentous fungi. The cell wall in *Olpidium radicale* is reported by Schwartz and Cook to be composed of cellulose. In many

species of this family, however, the cell walls do not give the typical cellulose reaction with chloriodide of zinc.

FAMILY WORONINACEAE.—In general appearance and life history the members of this family parallel closely those of the foregoing family (Olpidiaceae). They differ in the fact that the swarm-spores (Figure 12, D) possess two anteriorly inserted flagella (Cook and Nicholson) and in some species show a tendency toward diplanetism, i.e. they exist as two forms which encyst between the two stages. The composition of the cell wall is reported as being cellulose in *Olpidiopsis* and in *Woronina* and in a number of other genera. With few exceptions they occur as parasites in members of the Order Saprolegniales. One species is parasitic in the alga *Vaucheria*. Sparrow has studied several species parasitic upon marine Florideae. *Olpidiopsis*, (Figure 11) occurring in the filaments of Saprolegniaceae

resembles *Pseudolpidiopsis* very closely, even to its mode of sexual reproduction, but the swarm-spores are biflagellate instead of uniflagellate. *Woronina*, according to Cook and Nicholson, forms within the host filament a naked cell which by repeated division of the nucleus becomes a fairly large plasmodium (Figure 12, A). This divides up into many sporangia, the whole mass becoming pro-

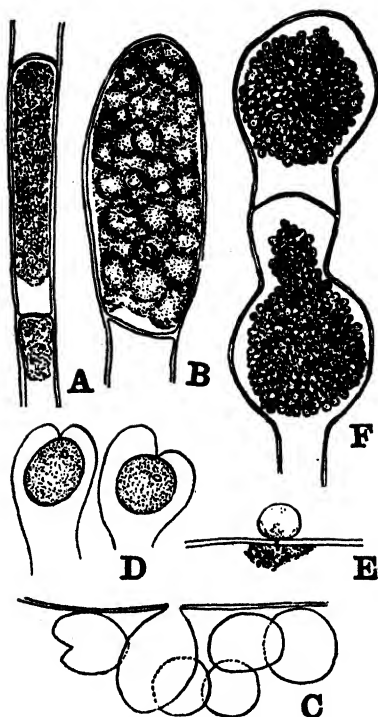


FIG. 12.—Chytridiales, Woroninaceae. *Woronina polycystis*. A, organism nearly filling host cell; B, division of organism into zoosporangia; C, empty zoosporangia, one showing exit tube; D, zoospores; E, infection of host by zoospore; F, cystosori within host. (After Cook and Nicholson, 1933.)

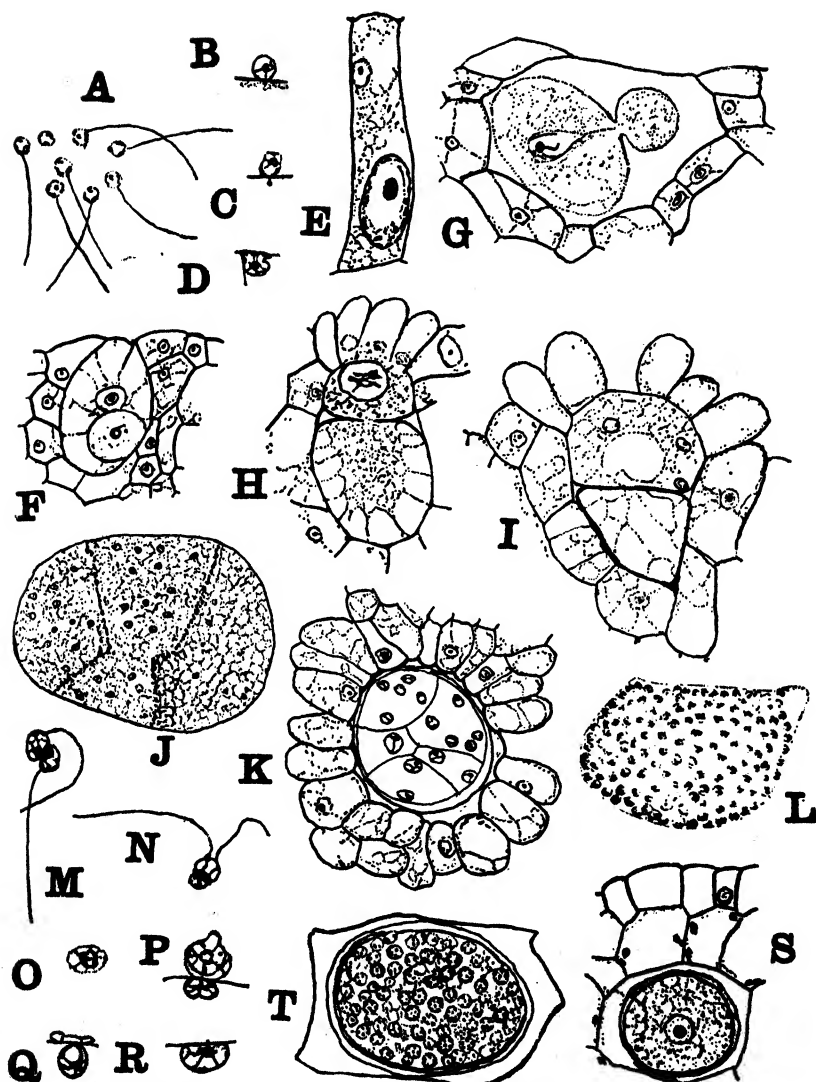


FIG. 14.—Chytridiales, Synchroniaceae. *Synchronytrium endobioticum*: A, zoospores; B, C, D, stages of infection of host cell; E, parasite in upper part of host cell; F, parasite enlarged; G and H, sorus emerging into host cell; I, nuclear division begins; J, segmentation begins; K, sorus containing five sporangia; L, sporangium containing swarm spores; M, N and O, stages in union of swarm spores; P, Q and R, infection of host cell by zygote; S, resting sporangium in host cell; T, resting sporangium producing swarm spores. (After Miss Cur, 1921.)

Two species of *Synchytrium* are of economic interest, *S. vaccinii*, causing small galls on the leaves and fruit of the cranberry (*Oxycoccus macrocarpon*) and *S. endobioticum*, the cause of the very destructive wart disease of the potato (*Solanum tuberosum*).

One or possibly two other genera occur as parasites in algae. One of these is *Micromyces* of which the species *M. zygonii* Dang. has been observed in America in *Spirogyra* by Couch. Its plant body is spherical with numerous long spines. Through a small opening the contents emerge and form a thin-walled vesicle which divides

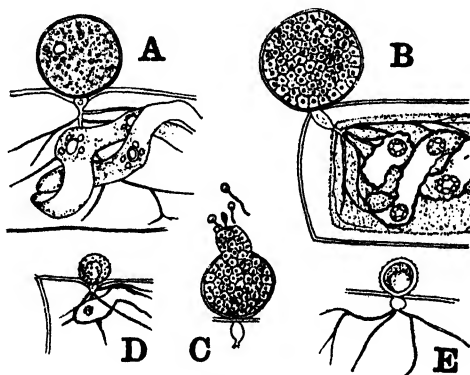


FIG. 15.—Chytridiales, Rhizidiaceae. *Phlyctochytrium hallii*. A, nearly full grown plant; B, zoospores distinctly differentiated; C, discharge of zoospores; D and E, resting sporangia. (After Couch, 1932.)

up into several sporangia. Within these are produced numerous uniflagellate swarm-spores which may infect the host directly or may unite by twos. The smaller, thick-walled resting spores, which are likewise spiny, are probably the product of infection by the zygotes, but this has not been proved. The resting spore germinates by the extrusion of a vesicle within which sporangia are produced.

FAMILY RHIZIDIACEAE.—As in the Olpidiaceae and Synchytriaceae the swarm-spores in this family are provided with but one, posterior flagellum (Figure 15, C). The swarm-spore encysts upon reaching its host and sends a haustorial process into the host cell, the main body of the encysted swarm-spore remaining outside. The haustorium may be a short undivided peg-like structure or slender and more or less branched (Figure 15, A, B), sometimes penetrating to other host cells as well. The external portion may enlarge

directly to form the zoosporangium or the latter may be formed above it or may arise as a swelling of the haustorium just beneath the host cell wall. The organism remains uninucleate until the sporangium begins to develop when the nucleus divides many times to form the nuclei of the swarm-spores. The haustorium does not at any time contain any nuclei and can hardly be considered as homologous to a mycelium. Resting cells (Figure 15 *D* and *E*) are produced in some species but their mode of origin is unknown. Sexual reproduction by the union of two well developed cells has been observed in some cases. Fusion of swarm-spores although possibly occurring has not been demonstrated. The host organisms are mostly algae, pollen grains or small aquatic animals. A few species are saprophytic.

Rhizophidium occurs in water on various substrata. It consists when mature of an enlarged, more or less spherical, thin-walled external sporangium with a usually tufted haustorium within the host cell. Upon the maturity of the numerous swarm-spores they escape through one or more pores in the sporangium wall. Sometimes the external cell becomes a thick-walled resting spore which produces its swarm-spores only after a wait of some time. Couch has shown for *R. globosum* that these resting spores arise as follows. A zoospore "comes to rest on the host, penetrates the wall, and develops apparently just like a sporangium. Later another spore comes and attaches itself to the larger body. . . . The smaller cell discharges its entire contents into the larger. . . . This now secretes around itself a thick wall and goes into the resting state." *Phlyctochytrium* grows on algae into which its much branched haustorium penetrates. This arises from a swelling (subsporangial vesicle) just within the host wall while the portion external to the wall enlarges to become the zoosporangium. Only the presence of the vesicle distinguishes this from *Rhizophidium* (Figure 15).

Harpochytrium occurs usually on *Spirogyra* and closely related algae. Its haustorium is a slender process terminated by a small disk in or on the host cell wall. The external portion of the fungus elongates to a slender, straight or curved sporangium many times as long as broad. In it the swarm-spores lie in one or two rows, escaping from an apical opening. A cell wall formed near the base separates the sporangium from a basal portion which, after the discharge of the swarm-spores, elongates to form a new sporangium.

either within the empty sporangial wall or externally to it at one side. Sexual reproduction is unknown.

Entophlyctis also grows on algae. It differs from *Rhizopodium* in that the sporangial swelling occurs inside the host cell, being connected by a very narrow process with the button-like structure which represents the original swarm-spore. The internal sporangium may become a thick-walled resting spore.

The genus *Polyphagus* is usually placed in this family but its connection with the other genera is doubtful. The single species *P. euglenae* (Figure 16) is parasitic on species of *Euglena* and other one-celled green organisms. Instead of being an internal parasite it lives externally. The germinating zoospore sends out in various directions slender processes (Figure 16, *A*) which penetrate the host cells that they encounter. Sometimes where the latter are crowded in considerable numbers as many as fifty may be attacked by the haustoria from the one parasite. The latter remains uninucleate and is invested by a firm thin wall. Within the swelling representing the original zoospore the nucleus divides to form the nuclei of the zoospores, and the whole contents bud out into a somewhat elongated thin-walled sack within which the division into the uninucleate zoospores takes place (Figure 16, *F, G*). As many as several hundred of the zoospores may be produced. Upon the occurrence of unfavorable conditions conjugation of two parasites may occur. A somewhat smaller (male) cell sends out a slender process (perhaps a modified haustorium?) and when this comes into contact with a larger (female) cell the process enlarges and the nucleus and contents of the whole parasite pass into this enlarged portion (Figure 16, *B, C*). Then the nucleus of the female cell also enters this cell and the wall thickens to form a thick-walled resting spore. After several months a zoosporangial sack is formed in which the nuclei fuse (Figure 16, *D, E*) and then divide to form the nuclei of the zoospores.

FAMILY CLADOCHYTRIACEAE (excluding Family Hyphochytriaceae).—The plants included in this family may perhaps be looked upon as a more complex development of the Rhizidiaceae. In the latter family the fungus is unicellular and at first uninucleate, with a more or less well developed rhizoidal (or haustorial) system. The enlargement containing the single nucleus becomes the zoosporangium. In the Cladochytriaceae (Figures 17 and 18) the nucleated enlargements are numerous, connected to one another by slender,

non-nucleate filaments the exact homology of which is not clear, though they remind one of the elongated rhizoids of *Polyphagus*.

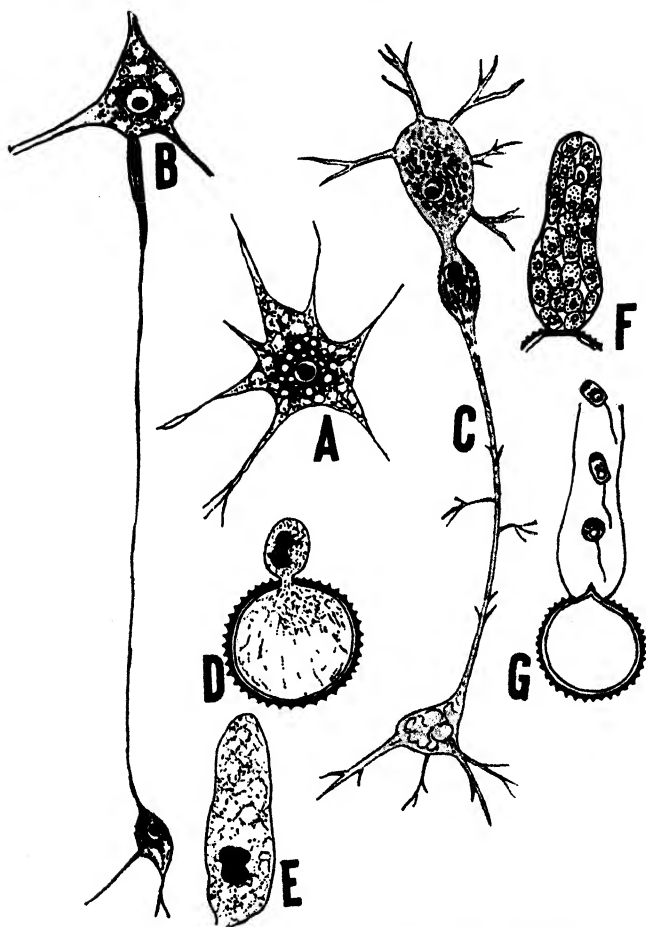


FIG. 16.—Chytridiales, Rhizidiaceae. *Polyphagus euglenae*. A, young vegetative cell; B, male cell conjugating with female cell by means of long extension; C, male nucleus has passed into the swelling destined to become the zygote; D, germination of the zygote, nuclei not yet united; E, union of gamete nuclei in young sporangium; F and G, development and escape of zoospores from zoosporangium. (After Wager, 1913.)

Each of these swellings may become a zoosporangium or may serve as a storage organ (Sammelzelle) out of which grow resting sporangia. Karling proposes the name rhizomycelium for the type of non-

nucleate filaments characteristic of this family. As in the Rhizidiaceae the zoospores are posteriorly uniflagellate (Figure 17, *H*).

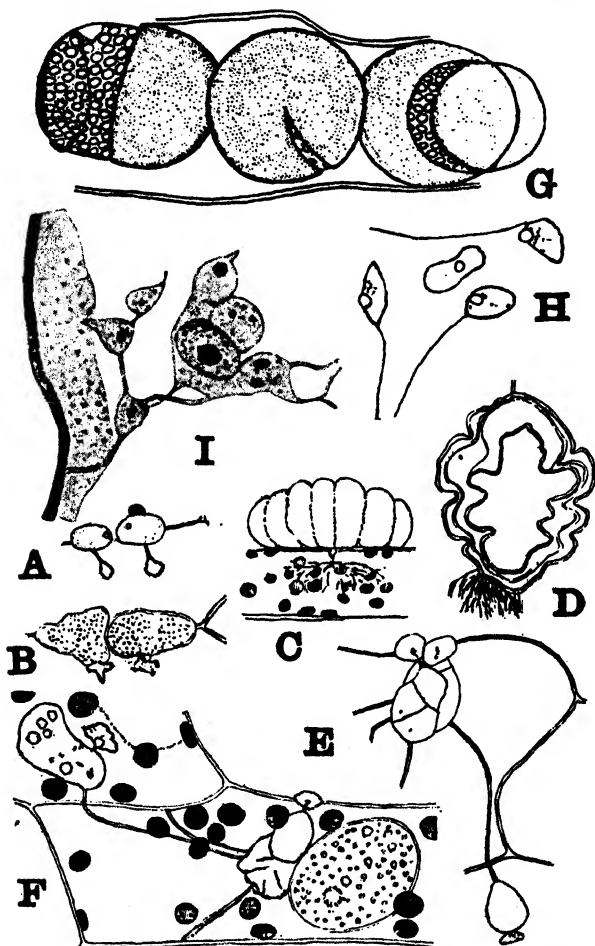


FIG. 17.—Chytridiales, Cladochytriaceae. A–G, *Physoderma maculare*. A–D, infection of host and formation of temporary zoosporangium; E, formation of "Sammelzellen" and rhizomycelium; F, formation of resting sporangium from "Sammelzelle"; G, mature dehiscing resting spore; H, zoospores; I, *Physoderma zeae-maydis* in tissues of corn leaf. (A–H after Clinton, 1902, I after Tisdale in Jour. Agr. Res., 1919.)

Sexual reproduction has been described for several forms but apparently erroneously in some cases. Thus in *Urophlyctis* the

supposed antherid and oogone have been proved to be respectively a "Sammelzelle" (Figure 18, *A*, *ta* and *tb*) and the resting zoosporangium (Figure 18, *A*, *rb* and *B*) which grows out of it. Cellulose has not been demonstrated in the cell walls of the few forms in which the test for this substance has been made. Bartlett suggests that possibly chitin is present in *Urophlyctis potteri* although he does not report making direct chemical tests.

Nowakowskiella and *Cladochytrium* occur as very slender branching filaments tapering to fine points, growing in the tissues of usually decaying vegetable matter. Here and there a swelling occurs which becomes a zoosporangium which opens by a lid in the first named genus and by a short exit papilla in *Cladochytrium*. Karling has shown recently that in *Cladochytrium replicatum* resting sporangia may be formed. These are of various sizes and shapes, conforming to the host cells within which they are formed. They become thick celled, the exterior of the wall producing up to 30 fine straight hyaline threads 4 to 9 microns long. A sporangial neck provides for the germination which consists of the formation and escape of numerous uniflagellate zoospores. *Catenaria* is parasitic in the eggs and bodies of small aquatic animals. Butler figures its development in liver-fluke eggs. The irregular zoosporangia are separated by narrow, usually septate, isthmuses. The zoospores escape through an exit tube. In *Physoderma maculare* (Figure 17, *A-H*) Clinton has shown that the germinating zoospore sends rhizoids into the host cell (submerged leaf of *Alisma*) and enlarges externally to become a zoosporangium much in the manner of *Rhizophidium*. After the zoospores escape through an exit papilla a second zoosporangium may be formed within the empty walls of the first, and so on two to four times. Other zoospores settling on older leaves or perhaps on leaves not permanently emerged send in a fine filament which swells to become a storage cell (or Sammelzelle) which produces haustorial processes or fine filaments which may penetrate to other cells and there, in their turn, produce similar cells, and so on. From such a cell there arises a bud which eventually becomes larger than the original cell, thick walled and somewhat flattened on one side. This is the resting sporangium which after a period of rest enlarges and bursts off the outer thick wall with a circular split, forming a very large lid, and forms an exit papilla on the thin inner wall, setting free the uniflagellate zoospores. The suggestion may be

made that possibly the zoospores are capable of functioning as gametes, the external zoosporangia arising from zoospore infection, the internal infection by zygotes. *Physoderma zeae-maydis* is sometimes destructive to corn (maize, *Zea mays*) in the southern part of the United States and in Asia. Usually only the internal rhizomycelium and the "Sammelzellen" (Figure 17, I) and resting sporangia are observed (Tisdale) but Sparrow has shown recently that it is possible to obtain the production of the external slipper shaped sporangia by placing pieces of young maize leaves in a hanging drop culture with the zoospores from the resting sporangia. As in *P. maculare* new zoosporangia are formed within the emptied older ones. The spores are markedly smaller than those arising from the resting sporangia and Sparrow suggests that they may possibly be gametes. Jones and Drechsler and also Bartlett have shown that *Urophlyctis* (Figure 18) has much the same life history as *Physoderma* but causes extensive gall production by the host, this being almost or quite absent with infection by *Physoderma*. The external zoosporangia have not been reported. Within the infected epidermal cell develops a "Sammelzelle" or "turbinate cell," at first uninucleate but soon plurinucleate. At its distal end is formed a terminal tuft of haustoria. At several places on the cell buds are formed into each of which a nucleus passes, following which the bud grows out as the end of a very slender non-nucleate filament. This enlargement in turn becomes a turbinate cell and may give rise to other similar cells, usually 3 to 5 cells from each. In the center of the distal tuft of haustoria there soon buds out a thin walled cell which grows rapidly and becomes much larger than the cell from which it grows. This becomes thick walled and bears a crown of haustoria (Figure 18, B). During its growth the cytoplasm and nuclei from the turbinate cell pass into it. This is not an act of fertilization. The connecting rhizomycelium soon disappears and finally only the resting sporangia are to be found in the gall tissue. After some time the sporangium is capable of germination. Scott has studied this in *U. alfalfae*. It produces 1 to 15 or more zoosporangia which escape through irregular fissures in the brown walls. These vary in diameter from 10 to 40 microns. Zoospores^{le} escape through a short exit papilla, there being formed sever^{eus} such papillae on a large sporangium. The zoospores are 4 t^{ntry}. microns long with a posterior flagellum 30 to 50 microns l^e con- nucleus

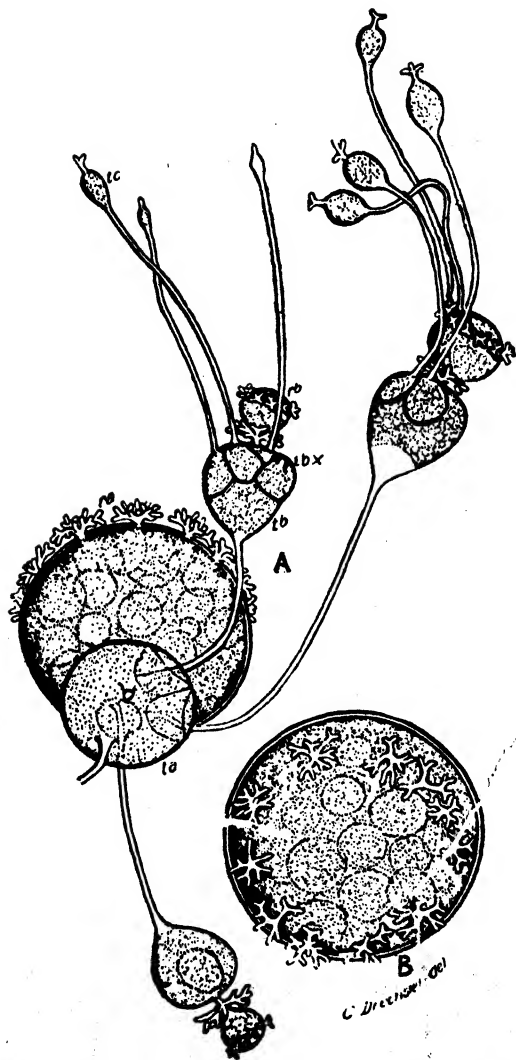


FIG. 18.—Chytridiales, Cladochytriaceae. *Urophlysis alfalfae*. A, rhizomorph, "Sammelzellen" (ta and tb) and resting sporangia (ra and rb); B, top view of resting sporangium. (After Jones and Drechsler, in Jour. Agr. Sci. 1920.)

Scott observed no conjugation of zoospores. On the other hand O. T. Wilson reports that the zoospores are biflagellate, one flagellum being very short, and that they are of two sizes. These conjugate before infection takes place. This needs confirmation as there is a possibility that the supposed zoospores or gametes may have been organisms parasitic within the resting sporangia of the *Urophlyctis*.

The relationships of the five families here included in the Order Chytridiales are uncertain. Except for the Family Woroninaceae the zoospores are provided with a single posterior flagellum, a fact that may be of significance as to their relationship to each other and to the Order Monoblepharidales. Yet if the Woroninaceae with their biflagellate zoospores belong in the Order Chytridiales we can not place too great emphasis upon the number and location of the flagella. Scherffel attempts to derive the families of this order from certain Protozoa, near the Family Pseudosporeae, which are amoeboid organisms which divide into zoospores. Two series are known, those with one and those with two flagella, and from these two series Scherffel derives the uniflagellate and biflagellate families of the Chytridiales. In deriving the Chytridiales from this family Scherffel is following Gobi who, according to Jaczewski, made a similar suggestion in 1891. Another alternative is to regard the Chytridiales as derived from some of the one-celled green algae. Some of the latter live endophytically within the intercellular spaces of higher plants that are aquatic or found in wet places. These endophytic algae possess chlorophyll and reproduce asexually by zoospores and sexually by the union of motile gametes. Both zoospores and gametes are provided with two anterior flagella. The genus *Rhodochytrium* (Figure 19) is closely related to these endophytic algae but lacks chlorophyll although containing a carotin-like substance, and retaining the ability to store starch as food. This plant is parasitic in a number of genera of plants (*Ambrosia*, *Spiranthes*, *Asclepias*). The zoospore settles on the epidermis of the host and encysts, then grows as a tube between the epidermal cells into the subepidermal intercellular spaces where it sends out rhizoid-like extensions (Figure 19, B) to the water-conducting tissues of the host and haustoria into the cells of the phloem. The single nucleus remains in the enlarged portion a little below the point of entry. A thin-walled zoosporangium may be produced into which the contents of the rhizoids are withdrawn. The greatly enlarged nucleus

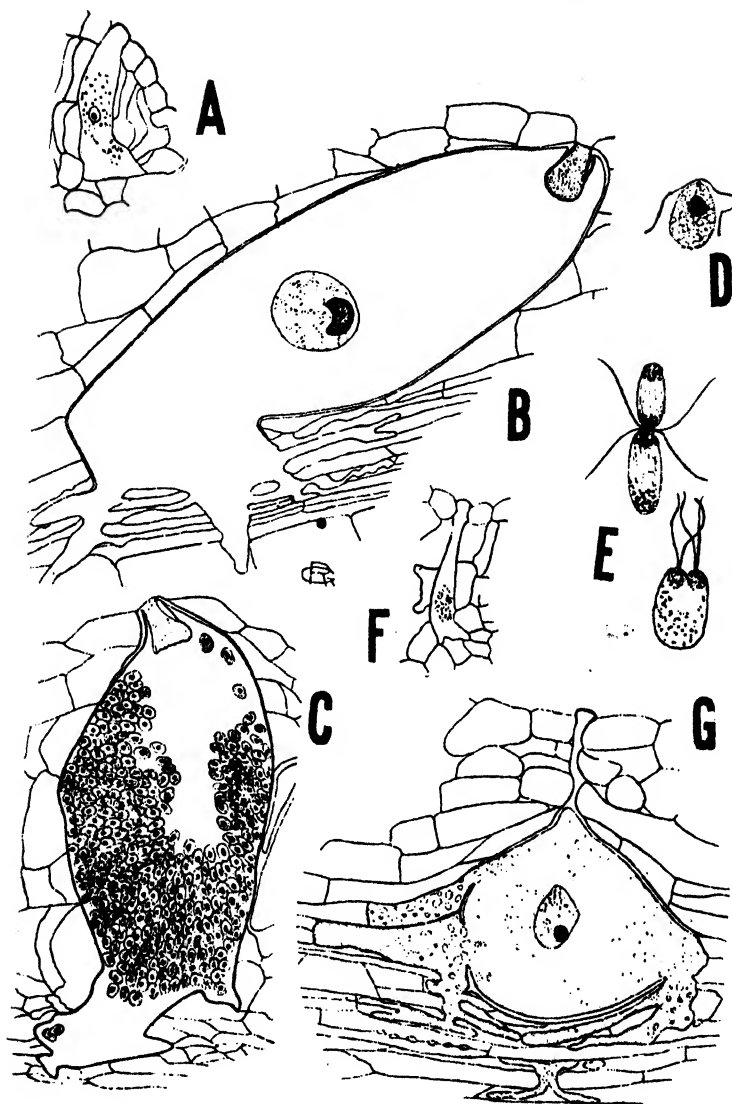


FIG. 19.—*Rhodochytrium spilanthis*. A, young sporangium; B, fully grown sporangium; C, mature sporangium; D, swarm spore; E, unites; F, young resting sporangium; G, fully grown resting sporangium. (After Griggs, 1912.)

then divides many times and finally numerous apically biflagellate zoospores are delimited (Figure 19, C) which escape to the exterior of the host. In the presence of plenty of water they swim as zoospores but with reduction of water supply they conjugate (Figure 19, E), to form a 4-flagellate zygote whose two nuclei quickly fuse. In addition to the thin-walled zoosporangia there occur thick-walled, uninucleate resting spores (Figure 19, F and G) which after several months produce zoospores which behave as do those from the thin-walled zoosporangia. Though there is no proof one is tempted to suspect that, as in *Synchytrium*, the resting spores arise from infections by zygotes and the thin-walled zoosporangia by infections from zoospores. Except for the absence of chloroplasts, *Rhodochytrium* resembles in structure and habit the alga *Phyllobium* which lives endophytically in various hosts. In *Phyllobium* the gametes though both motile differ somewhat in size. This, in turn, differs from *Chlorochytrium* in the presence of the tube-like extensions while in the latter the cell-body is rounded. All these possess but one nucleus until the nuclear division begins preparatory to production of zoospores. *Chlorochytrium* except for its endophytic habit resembles some of the free-living one-celled Chlorophyceae. Thus we have a rather close series from the latter to forms like *Synchytrium* except for the gap, difficult to explain away, caused by the difference in zoospore structure and habit. In *Synchytrium* the zoospore has a single posterior flagellum and in these other organisms they have two anterior flagella. The derivation of the Family Woroninaceae from this series is not as difficult, as their zoospores are biflagellate. Still another alternative is to consider some or all of the Chytridiales to be reduced from filamentous Monoblepharidales and Saprolegniales, a view which has considerable in its favor.

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CHAPTER III

FILAMENTOUS FUNGI—PHYCOMYCETEAEE: MONOBLEPHARIDALES, SAPROLEGNIALES

A true mycelium consists of non-septate, multinucleate coenocytic hyphae or of filaments with septa dividing them into uninucleate or binucleate cells or into short coenocytic segments. Only rarely is a mycelium unbranched. Growth in length is mostly confined to the terminal portion of the filament. Intercalary growth is ordinarily not found except near the ends of the hyphae. Branches may arise by renewed growth-activity as lateral outgrowths even from old hyphae where elongation has long since ceased. On the other hand branching may originate, and probably more often does so originate, in the younger, still growing portions of the hyphae.

The fungi included by the author in the Class Phycomyceteae excluding the Order Chytridiales which lack mycelium and are believed to be more properly omitted from the class, are forms with true mycelium, typically of the non-septate, coenocytic type. Deviations from this type occur in some of the more specialized groups of the class and will be discussed when these groups are considered. The hyphae of many of the aquatic forms are relatively large, occasionally attaining a diameter of over 100 microns, although this is far above the average. The nuclei are small and numerous and scattered throughout the parietal layer of cytoplasm. The central portion of the filament is usually occupied by a large vacuole. Streaming of the cytoplasm is often observable in the more actively growing portions of the mycelium. Although cross walls are usually lacking in healthy, actively growing vegetative mycelium (but see *Alloomyces* for an exception) an injury usually leads to the production of septa which delimit the injured portion. The presence of toxic substances in the surrounding medium may cause excessive formation of septa. In general the whole class is extraordinarily sensitive to the toxic effects of even small quantities of copper compounds (Horn).

The cell walls of the Phycomyceteae are basically composed of carbohydrate compounds. These are cellulose and pectic compounds in the aquatic and soil inhabiting Monoblepharidales and Saprolegniales and in the endoparasitic Peronosporales. In the Mucorales and Entomophthorales there is a conflict of opinion as to the composition of the walls. Mangin and Hopkins find, in various Mucorales, true cellulose in addition to callose and pectic substances. von Wettstein, on the contrary, declares that no true cellulose occurs but that chitin is present in the Mucorales and Entomophthorales.

In the larger forms that are not highly specialized parasites there may be distinguished two types of mycelium, the nutritive or trophic mycelium within the substratum and a more or less extensive external mycelium upon which are borne the asexual and often sexual reproductive organs. The former type of mycelium is repeatedly branched, the successive branches rapidly decreasing in diameter and often tapering to sharp points, while the external mycelium may be unbranched or relatively little branched, and sometimes uniform in diameter, much thicker than the trophic mycelium. This external mycelium may be cylindrical or may be constricted at intervals but without septa (except *Allomyces*). Sometimes there is a large supporting or storage body from which emerge slender hyphae bearing the reproductive organs. The plant parasitic forms such as the Peronosporales produce true haustoria which penetrate the host cells between which the mycelium passes.

Asexual reproduction is by the formation of zoospores in terminal zoosporangia or by a modification of this process. The cytoplasm and contained nuclei flow into the terminal portion of a hypha and this then usually becomes separated from the remainder of the hypha by a cross wall. The numerous nuclei divide further and cleavage vacuoles divide the cytoplasm into numerous naked blocks containing one to a few nuclei each. In the unmodified zoosporangia these naked masses round up and develop 1 or 2 flagella and escape from an opening in the zoosporangium wall, usually by the dissolution of a portion of the wall at or near the apex.

Sexual reproduction within the class varies from apparently isogamous to heterogamous types. Gametangia are cut off at the apices of the main hyphae or special branches in a manner similar to that in the formation of zoosporangia. The uniting gametes

may both be flagellate (*Allomyces*) or the female gamete may be non-flagellate and be fertilized within the oogone by a flagellate sperm (*Monoblepharis*) or the smaller antherid may become attached to the larger oogone and the sperm nuclei enter the latter through a conjugation tube (Saprolegniales, Peronosporales), or unequal or apparently equal gametangia may meet and their contents fuse (Mucorales, Entomophthorales). The resultant zygote may remain naked or thin-walled (*Allomyces*) but usually forms a thick-walled oospore within the oogone or a thick-walled zygosporangium usually occupying the cavities of the two uniting gametangia (Mucorales).

The Phycomyceteae are usually divided into two sub-classes on the basis of the manner of sexual reproduction: Oomyceteae, with gametes or gametangia manifestly unequal, the oospore escaping or lying in the oogone, and Zygomyceteae, with the gametangia mostly equal (a number of striking exceptions) and the zygosporangium usually but not always occupying the cavities of *both* gametangia and fused with the wall of the latter. In the Sub-class Oomyceteae zoospores are typically formed in asexual reproduction (although often modified or absent): in the Sub-class Zygomyceteae zoospores are never formed. According to von Wettstein cellulose is confined to the Oomyceteae and chitin to the Zygomyceteae, but Mangin and Hopkins do not agree with him. Hopkins reports true cellulose in Mucorales.

The Oomyceteae are divided variously into from two to six orders. The author takes a middle stand and recognizes here three orders, admitting that this standpoint will doubtless have to be modified with the acquisition of further knowledge of the life-histories of many of the poorly-known forms. Following Minden, Kniep, Fitzpatrick and others, the aquatic and soil-inhabiting forms are divided into two groups. The Blastocladiaceae, Monoblepharidaceae and, doubtfully, the Hyphochytriaceae are placed in one group and the Saprolegniaceae, Leptomitaceae and Ancylistidaceae in the other. Whether the three families first mentioned should form two orders, Blastocladales and Monoblepharidales or but one order is a matter that further study must decide. For the present the author prefers to have *Monoblepharidales* as one order, the *Monoblepharidales*. The other three ~~will cross~~ the Order Saprolegniales, although some authors divide ~~in which the~~ three orders, Saprolegniales, Leptomitales and Ancylistidales that under is very possible that the relationship of some of

the genera now assigned to the Blastocladiaceae and Leptomitaceae may be found to be closer than is indicated by the division made above. Standing apart from these two orders but much closer to the Saprolegniales are the endoparasitic Peronosporales, found as internal parasites in land plants. The three orders named may be distinguished as follows:

Order Monoblepharidales.—Zoospores with 1 posterior flagellum; cell wall not giving cellulose reaction with chloriodide of zinc until after treatment with KOH solution to remove a masking substance (not chitin). Cytoplasm often clearly reticulate in appearance. Zoosporangia not separating from the supporting hyphae. Aquatic or in moist soil, saprophytic on vegetable matter, less often on animal matter.

Order Saprolegniales.—Zoospores pear-shaped with 2 anterior flagella or kidney shaped with two lateral flagella attached to the concave side and directed, one forward, the other backward; the cell wall showing the cellulose reaction immediately upon the treatment with chloriodide of zinc. Cytoplasm not conspicuously reticulate. Zoosporangia not separating from the supporting hyphae. Aquatic or in moist soil, mostly saprophytic on vegetable matter or more rarely on animal matter, some species parasitic upon algae, others upon aquatic animals, a few upon the roots of higher plants.

Order Peronosporales.—Zoospores kidney shaped as described for the preceding order; cell wall giving the cellulose reaction immediately upon treatment with chloriodide of zinc. Zoosporangia mostly separable and wind borne (i.e. acting as conidia) only producing their zoospores after dropping into water or germinating directly by a germ tube without producing zoospores. Internal parasites in land plants, a few species capable of maintaining themselves as saprophytes in the soil or as parasites on algae, etc. This order will be discussed in the next chapter.

The three families and about thirty species here recognized in the **Order Monoblepharidales** need much further study. In both the Blastocladiaceae and the Monoblepharidaceae species have been described as possessing two flagella. Should this be confirmed the chief distinction between this order and the Saprolegniales will fall. However, the researches of Cotner show that at least one species the presence of two flagella is due to unfavorable a manner such biflagellate zoospores possessing two nuclei and uniting giving in

reality two zoospores that because of unfavorable conditions have failed to separate. So the author for the present maintains this distinction, in the belief that future researches will throw more light on the subject.

In the BLASTOCLADIACEAE the following forms may be considered: *Gonapodya* (Figure 20) is saprophytic on vegetable matter and consists of much branched filaments strongly constricted at frequent intervals so as to give the appearance of a string of elongated beads.

The narrow isthmuses between the segments are sometimes plugged by masses of cellulin, a form of carbohydrate found also in the Family Leptomitaceae. The terminal segments become enlarged in diameter and elongated, narrowing toward the tip and their contents divide into a number of posteriorly uniflagellate zoospores which escape through an opening at the apex. After the escape of the zoospores the segment below grows up into now empty zoosporangium and forms a new zoosporangium. Sexual reproduction is unknown. The genus *Allomyces* consists of soil inhabiting or aquatic fungi saprophytic on animal or plant matter. The internal trophic mycelium is that typical for the class. The external mycelium consists of a thick basal piece which branches in an almost dichotomous manner, a pseudoseptum occurring at the base of each branch and at intervals elsewhere. These pseudosepta arise in

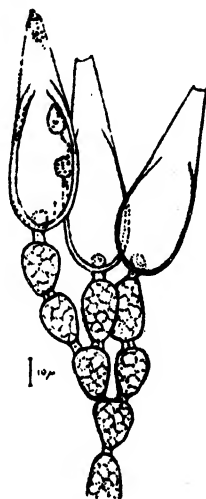


FIG. 20.—Monoblepharidales. *Gonapodya prolifera*. (After Sparrow, 1933.)

the manner usual for fungus septa but leave large perforations through which the protoplasm is continuous. From the ends of the branches of the second or third order arise two or more slender hyphae which terminate in ovoid zoosporangia with several exit papillae. These hyphae branch sympodially so that the zoosporangia may come to appear lateral in attachment. Sometimes the zoosporangia are catenulate. On the older plants thick-walled resting sporangia are also produced. These are set free and after weeks or months the thick wall cracks open and the inner wall develops exit papillae through which the zoospores escape. In *Allomyces javanicus* Kniep observed that under certain conditions there arose alternately smaller

and larger gametangia forming a chain two to five elements in length. From these emerged uniflagellate gametes, similar in appearance but differing in size. They fused at once. If kept apart they did not

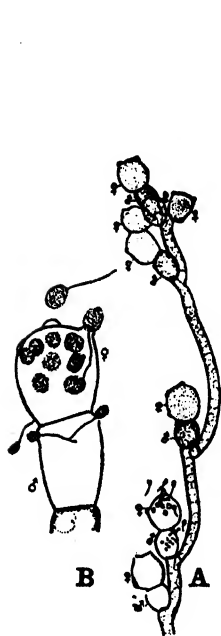


FIG. 21.

FIG. 21.—Monoblepharidales, *Allomyces arbuscula*. A, habit sketch of hypha showing clusters of male and female gametangia; B, gametes escaping from gametangia. (After Hatch, 1933.)

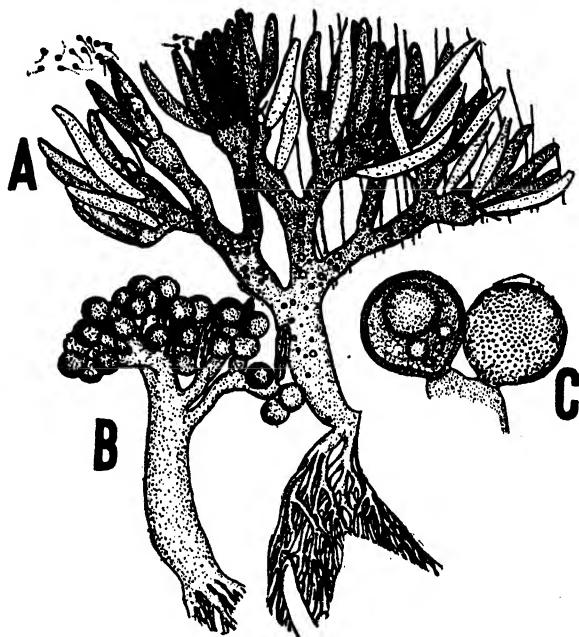


FIG. 22.

FIG. 22.—Monoblepharidales, *Blastocladia pringsheimii*. A, plant bearing thin-walled zoosporangia; B, plant bearing numerous thick-walled and a few empty thin-walled zoosporangia; C, thick-walled zoosporangia in detail. (After Thaxter, 1896.)

develop parthenogenetically but soon died, showing that they were different from the zoospores which under identical conditions of light and temperature germinated in the usual manner. Kniep reports that the zoospores from the thin-walled zoosporangia give rise to sporophytes, but those produced from the thick-walled zoosporangia developed into gametophytes. The occurrence of sexuality has been confirmed for *A. arbuscula* by Hatch, (Figure 21) who also noted a difference in color between the male and female gametangia. He also observed that the zoospores from the thick-walled zoosporangia gave rise to the sexual plants.

In *Blastocladia* (Figure 22) the plant body is quite similar but there are no constrictions or pseudosepta in the more or less dichotomously branching external mycelium, and the zoosporangia have but one exit papilla. The basal segment is usually considerably enlarged, sometimes even globose. Resting sporangia similar to those in *Allomyces* are produced in this genus. Sexual reproduction is unknown except in the doubtful case of *B. globosa* in which Miss

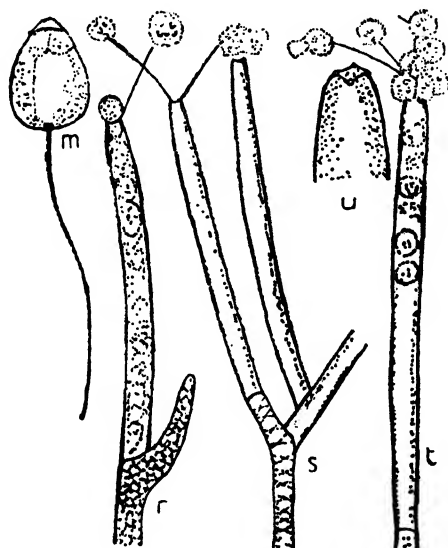


FIG. 23.—Monoblepharidales. *Monoblepharis polymorpha*, asexual reproduction. (After Sparrow, 1933.)

Kanouse observed once an antherid-like structure at the end of a slender hypha. As this was not in contact with an oogone its sexual function was not proved. The seven or more species of *Blastocladia* are aquatic fungi saprophytic on vegetable matter. By suspending fruits of apple, hawthorn, etc. in streams or pools it is often possible to obtain abundant growth of *Blastocladia*.

Monoblepharis is the best known genus of the group and is the only genus of the FAMILY MONOBLEPHARIDACEAE. It occurs on twigs and other vegetable matter in water, especially in the early spring before the water becomes too warm. The external mycelium is slender and not conspicuously branched (Figure 24, A). Such branching as occurs is mostly in connection with the formation of

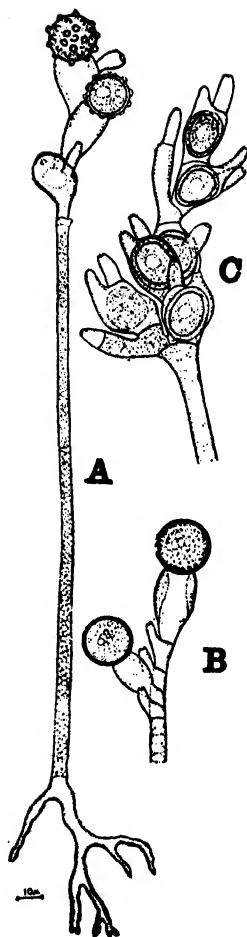


FIG. 24.—Monoblepharidales. A, *Monoblepharis polymorpha*, showing empty epigynous antherids and two exogenous oospores; B, *M. macrantha* var. *laevis*, showing three hypogynous antherids and two exogenous oospores; C, *M. fasciculata*, showing epigynous antherids and endogenous oospores. (After Sparrow, 1933.)

zoosporangia and sexual organs and is mostly of the sympodial type. The zoosporangia are terminal or may be found below the oogones. They are rarely wider than the supporting hyphae and produce a not very large number of rather large zoospores (Figure 23). In some species these are clearly uniflagellate but in others they have been reported to be biflagellate. In view of Cotner's observation (mentioned above) it seems best for the present to consider these biflagellate zoospores as not typical but due to improper temperature relations. The oogones are single and terminal, or several clustered at the apex of the mycelium, or in a chain (Figure 24). The antherid may be formed as a segment of the mycelium, immediately below the oogone (Figure 24, B) or may be terminal, the oogone being formed just below it so that the antherid appears to have budded from the oogone (Figure 24, A and C) or it may be produced on a separate male plant. From the beginning the oogone possesses but one nucleus. When the egg is ready for fertilization the apex of the oogone forms an opening through which the uniflagellate sperm enters. After fusion of egg and sperm the nuclear fusion may be long delayed. The fertilized egg either forms a thick-walled oospore within the oogone or creeps to its mouth and forms the thick-walled oospore there. Germination of the oospore is by means of a germ tube following the fusion of the gamete nuclei and the subsequent division (probably including meiotic division) of the zygote nucleus into 8 to 16 nuclei.

FAMILY HYPHOCHYTRIACEAE.—This is a group of illy known fungi, possibly related to the Monoblepharidales, but also perhaps

related to the Chytridiales. The true nature of their mycelium is yet to be determined, i.e., whether a true coenocytic mycelium or merely a non-nucleate rhizomycelium such as occurs in the Cladochytriaceae. The following genera are described and figured as having a rather

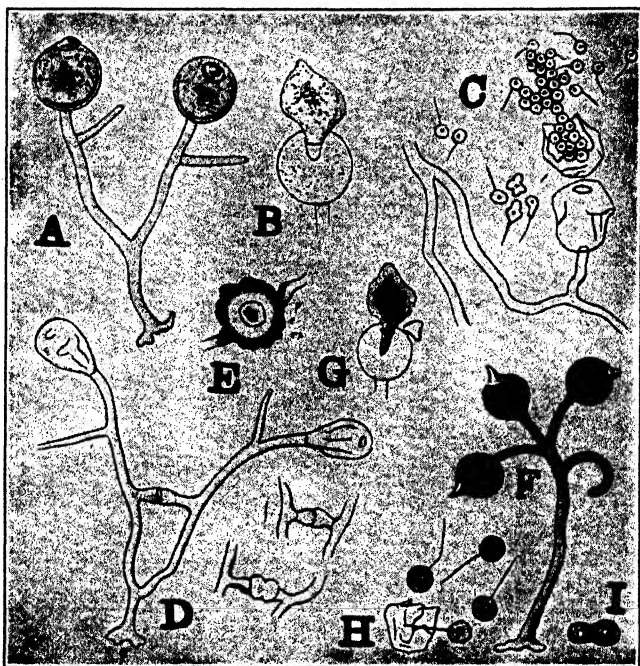


FIG. 25.—Monoblepharidales, Hyphochytriaceae. A-E, *Zygochytrium aurantiacum*. A, mature plant with two operculate zoosporangia; B, escape of contents from zoosporangium as a free vesicle; C, zoospores formed from vesicle; D, beginning of sexual reproduction; E, mature zygospore; F-I, *Teurachytrium triceps*. F, mature plant with operculate gametangia; G, emergence of vesicle; H, escape of gametes; I, union of gametes. (After Sorokin, 1874.)

well developed mycelium but no studies have been made as to their structure or the composition of the cell wall. *Macrochytrium* grows saprophytically on decaying matter. It consists of a large external zoosporangium arising from a tuft of short branching hyphae in the interior of the substratum. The zoospores escape through an opening formed by a large lid. Until cytological studies show that the mycelium is really nucleate and that this is not a uninucleate organism it can not be definitely decided whether this genus even belongs

here. Possibly it is one of the Chytridiales. *Tetrachytrium* (Figure 25, F-I) and *Zygochytrium* (Figure 25, A-E), observed but once by their discoverer, Sorokin, in Russia, are forms placed here for want of further knowledge. They are soil fungi with a rhizoidal holdfast and an upright stout and few branched mycelium bearing terminally on each branch a spherical, operculate sporangium or gametangium. The former produces motile equal uniflagellate gametes as well as uniflagellate zoospores; the latter produces zygospores in a manner very suggestive of the Mucorales, while the spherical zoosporangia produce uniflagellate zoospores. *Hyphochytrium* observed but once, by its discoverer Zopf, produces distantly septate hyphae with terminal and intercalary almost spherical, rather thick walled zoosporangia within which are produced numerous uniflagellate zoospores. The fate of these, whether true zoospores or gametes is unknown. The fungus was described from apothecia of a species of *Helotium*. One or two other genera may possibly belong in this family.

Because of the apparently true mycelium it is suggested that this family of ill assorted forms may represent reduced forms of the Monoblepharidales or perhaps, on the other hand, transitional forms from the Cladochytriaceae to this order.

Order Saprolegniales.—The fungi making up this group are perhaps more certainly interrelated than those included in the foregoing order. They possess well-developed coenocytic hyphae (except in the clearly reduced Family Ancylistidaceae) and give a sharp cellulose reaction upon treatment with chloriodide of zinc. The zoospores are biflagellate. Sexual reproduction is known for most of the genera and consists in the fertilization of one or more eggs contained in an oogone by a conjugation tube from an adhering antherid which may arise from the same plant (homothallic species) or from a male plant (heterothallic species). Parthenogenesis is met frequently in the order. The young eggs are multinucleate when first differentiated, in contrast to the uninucleate condition in *Monoblepharis*. The majority of the nuclei migrate to the outer portion of the egg and ultimately disintegrate, leaving one nucleus to each egg. The species are largely saprophytic, more often, perhaps, upon vegetable matter, but in some cases occurring in animal matter. A few species are parasitic upon fish fry in fish

hatcheries and some are root parasites. The three families and approximately 120 species may be distinguished as follows.

FAMILY SAPROLEGNIACEAE.—Mycelium extensive; cylindrical, not constricted, eggs single or numerous in the oogone, without periplasm; mostly saprophytic.

FAMILY LEPTOMITACEAE.—Mycelium extensive; cylindrical and constricted at regular intervals or consisting of a large basal supporting or storage body from which arise slender, usually regularly constricted, hyphae which bear the reproductive organs; saprophytic so far as known.

FAMILY ANCYLISTIDACEAE.—Mycelium reduced to short unbranched or branched intracellular tubes which soon become divided by septa into the reproductive organs. Parasitic, mostly in algal cells, rarely in pollen grains, nematodes and other organisms.

The members of the **FAMILY SAPROLEGNIACEAE** are in some cases strictly aquatic, but a considerable number of species are soil inhabitants. Contrary to the earlier belief they are mostly saprophytic on vegetable matter, less often on animal matter. Only a few species of *Achlya* and *Saprolegnia* are sometimes destructive to young fish in fish hatcheries. Several species of *Aphanomyces* and one or two other genera are parasitic on the roots of higher plants.

In about half of the *genera* of the family the oogone contains but one egg (Figure 26, C, E; Figure 27), but the pluriovulate *species* are far in the majority. The number of eggs per oogone in these may vary from two or three up to 50 in some species of *Saprolegnia* and *Achlya* (Figure 28). Fertilization of the eggs is accomplished by the passage of sperm nuclei, one to each egg, through conjugation tubes that penetrate the oogone wall from the adhering antherids

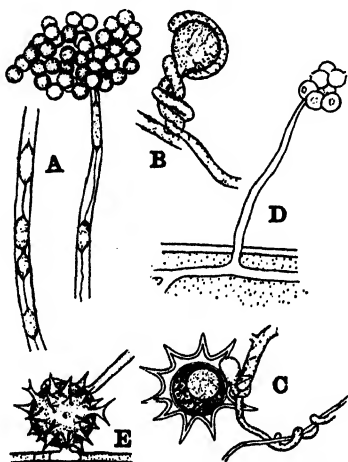


FIG. 26.—Saprolegniales, *Aphanomyces*. A-C, *A. exoparasiticus*. A, encysted zoospores at mouth of zoosporangium; B, young oogone and antherid; C, mature oogone containing oospore. D-E, *A. sp.* D, discharged zoosporangium; E, oogone and antherid. (A-C after Couch, 1926, D-E after Sparrow, 1930.)

(Figure 27). A single tube may branch within the oogone and so fertilize more than one egg. Sometimes several antherids may become attached to a single oogone. The fertilized egg forms a thick wall and becomes an oospore. In some cases although antherids are present there seems to be no conjugation tube so that the egg develops parthenogenetically. In some species antherids are only rarely formed or are entirely unknown. In *Brevilegnia dictyna*

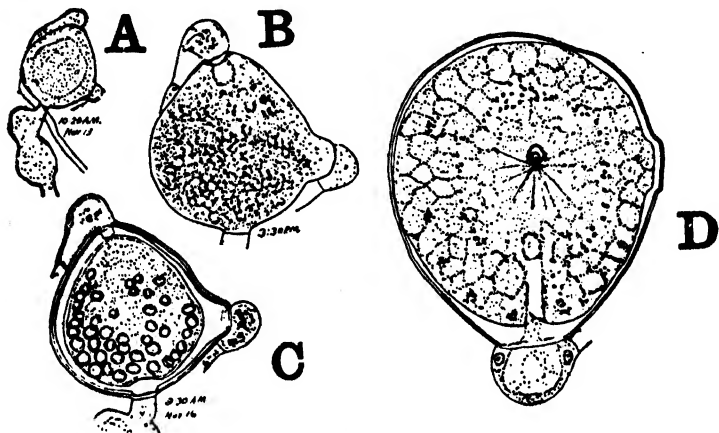


FIG. 27.—Saprolegniales. *Leptolegnia caudata*, stages in sexual reproduction. A, young oogone on stout hypha and two antherids from slender hyphae; B, same structures five hours later, one antherid discharging contents into oogone; C, same structures two and a half days later, oospore thick-walled; D, entry of sperm nucleus into egg, note peripheral supernumerary nuclei in both oogone and antherid. (After Couch, 1932.)

Cooper has shown that an opening is formed between the antherid and oogone but no conjugation tube.

It is difficult to determine whether the pluriovulate condition is the more primitive or a derived condition. If the Saprolegniaceae have arisen from some alga related to *Vaucheria*, either directly or through a fungus close to *Monoblepharis* the uniovulate condition would seem to be more primitive. On the other hand from a fungus like *Allomyces* with numerous motile megagametes produced in a single gametangium there might have arisen forms with numerous non-motile eggs, thus giving rise to the pluriovulate oogone such as occur in *Saprolegnia* and *Achlya*. The author is inclined to favor the first hypothesis and to consider the pluriovulate condition as derived from the uniovulate condition.

Apparently the primitive form of zoospore in this family is pear-shaped with two equal anterior flagella. Such zoospores only, are formed in two of the three known species of *Pythiopsis*. Far more frequently two types of zoospores are produced, the primary zoospores like those just described, which after an interval of swimming encyst and in a few minutes or hours give rise to the secondary zoospores which are kidney-shaped with the two flagella, one pointing forward, one backward, attached to the concave side. Fungi possessing these two types are said to be diplanetic in contrast to those with but one type which are monoplanetic. A few forms are known in which only the secondary type of zoospore is produced. Other forms show various modifications of the typical diplanetic scheme.

The zoosporangia are typically terminal segments of hyphae. When the zoospores are discharged a new zoosporangium may arise by proliferation, i.e. by the upward bulging of the basal septum of the old zoosporangium until a new zoosporangium is formed within the empty wall of the old one. When this is empty another and another may be formed within its empty walls so that the last formed may be surrounded by the empty walls of five or six preceding zoosporangia. In other cases the supporting hypha grows sympodially, forming a lateral shoot just below the old zoosporangium which, by the straightening of the hypha may come to have a lateral position although originally terminal.

The zoosporangium may be slender (Figure 26), like the supporting hypha, or clavate (Figure 28) or ovoid. Under certain cultural conditions the hypha may form ovoid or clavate zoosporangia in chains, each opening by an exit pore near its apical end. Under some conditions such potential zoosporangia round up into somewhat thick-walled resting spores or chlamydospores.

Emergence of the zoospores is usually through the softened apex of the zoosporangium. In *Saprolegnia*, *Leptolegnia* and *Isoachlya* the primary zoospores swim away as soon as released, encysting separately at some distance from the zoosporangium. In *Achlya*, *Aphanomyces* and several other genera the escaping primary zoospores encyst immediately upon emerging and form a ball of cells (Figure 26, *A*, *D*; 28, *F*) which later release the secondary zoospores. In *Thraustotheca* (Figure 28, *A*, *B*) and other genera the primary zoospores encyst within the zoosporangium and upon the rupture of

the latter as the spores swell the encysted spores escape and give rise to the secondary zoospores. In *Dictyuchus* (Figure 28, C) the encysted spores are polyhedral by mutual pressure and germinate within the zoosporangium by short exit tubes which penetrate the

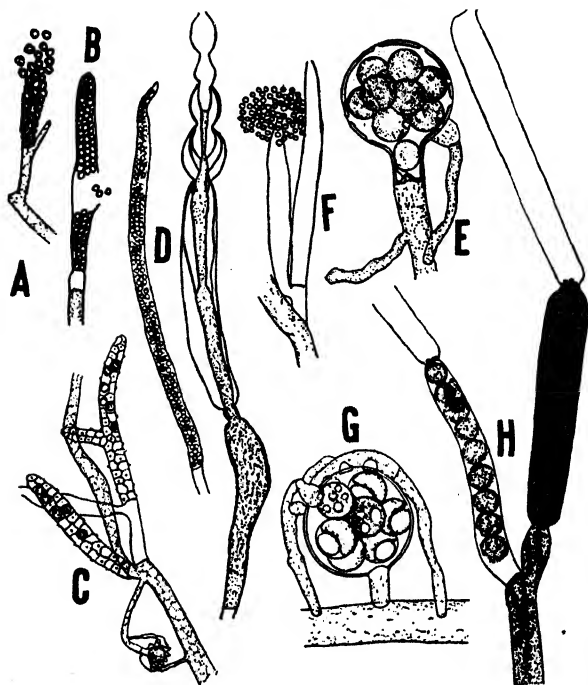


FIG. 28.—Saprolegniales. A and B, *Thraustotheca unispërma*; C, *Dictyuchus achlyoides*; D, *Saprolegnia monoica* var. *glomerata*, proliferated zoosporangia; E, oogone and antherid; F, *Achlya americana*, empty zoosporangia and encysted zoospores; G, oogone and antherids; H, *Leptomitilus lacteus*. (A and B after Coker and Braxton, 1926, C after Coker, 1927, D-H after Coker, 1923.)

zoosporangium walls, thus setting free the secondary zoospores individually. In *Aplanes* and *Geolegnia* and other genera the encysted primary spores germinate by germ-tubes within the zoosporangium or after the latter has disintegrated. Under varying conditions of culture the same species of *Saprolegnia* or *Achlya* may be induced to produce its zoospores in the manner typical of *Saprolegnia*, *Achlya*, *Thraustotheca* or *Aplanes*, respectively, showing that these modifications are not of very deep fundamental importance.

Pythiopsis.—In this rarely studied genus the sympodially produced sporangia may be ovoid (*P. cymosa*) or slender. The mycelium is rather stout as is typical for the family. The zoospores which escape are of the primary type. After encysting they may germinate by a germ tube or may produce zoospores again, but these are still of the primary type in two species and, according to Harvey, of the secondary type in the third known species. The oogone usually has but one egg. The antherids may be up to three in number and may arise from immediately below the oogone. The species of this genus occur in soil or in fresh water.

Saprolegnia (Figure 28, *D, E*) is the most commonly studied genus of the family. It contains about 20 species, mostly saprophytic, rarely parasitic, on animal or vegetable matter in water. Dead insects or even larger animals become surrounded by a fringe of the long external hyphae, the much branched trophic hyphae being within the animal tissues. These external hyphae are fairly stout (up to 50 to 100 microns in diameter in extreme cases) and more or less straight and but little branched. They terminate in club-shaped zoosporangia within which numerous zoospores are present in no definite arrangement. The primary zoospores squeeze out one by one from the terminal opening and swim away, encysting at a distance. The new zoosporangia form by proliferation within the empty ones. Usually a little later, under conditions which can be controlled in culture, short lateral branches arise which swell at the apex into a globular oogone separated by a septum from the main hypha. The oogone may be single or there may be a chain of several oogones in one hypha. Within the multinucleate oogone the protoplasm cleaves into several or many masses which round up to form the naked eggs (oospheres). These are at first multinucleate but soon all the nuclei but one disintegrate. On longer usually more slender branches from the same plant (often arising just below the oogone) or from a different plant are produced the antherids. These are terminal, multinucleate structures, somewhat larger in diameter than the supporting hyphae, from which they are separated by a septum. Upon reaching an oogone they become flattened against its outer surface. From the center of the surface of contact a papilla pushes into the oogone, forming the conjugation tube which seeks out an egg or branches so as to reach several eggs. A single sperm nucleus passes into each egg when fertilization actually takes place.

In many cases there is no fertilization and the egg becomes a thick-walled oospore parthenogenetically. After the disintegration of the oogone the oospore may lie dormant in the mud for several months, eventually germinating by a tube which may or may not be terminated by a zoosporangium. Reduction division probably occurs as the oospore germinates.

Achlya (Figure 28, F, G) with about 25 species, resembles *Saprolegnia* in habit and manner of growth. The chief morphological difference is that the hyphae bearing the zoosporangia grow sympodially so that there is no proliferation of zoosporangia. The behavior of the zoospores is also characteristic. The primary zoospores encyst immediately as they emerge from the mouth of the zoosporangium, forming a very typical cluster of encysted spores at its mouth. Only after 15 to 45 minutes or longer do these spores give rise to secondary zoospores. The oogones are usually pluriovulate and in all respects resemble those of *Saprolegnia*. Many species are parthenogenetic.

Both of these genera are exceedingly sensitive to minute traces of copper salts as discovered by Horn in 1903.

Aphanomyces (Figure 26) has slender zoosporangia with but a single row of zoospores which behave on emerging as do those of *Achlya*. The oogone has but a single egg. The species of this genus are parasitic in algae and the roots of higher plants, where they may cause root-rots.

Dictyuchus resembles *Saprolegnia* and *Achlya* and like them produces clavate zoosporangia. These may be single or may be formed in short chains or sympodially. They may fall off from the supporting hyphae, carrying with them the encysted primary zoospores. These germinate as indicated above, by the production of secondary zoospores, which may again encyst and emerge as similar zoospores several times. The oogone is usually uniovulate although in *D. polysporus* it is reported as pluriovulate. Some species of *Dictyuchus* are aquatic and some are found in the soil. Both homothallic and heterothallic species are known in this genus (Couch; Coker and Braxton).

FAMILY LEPTOMITACEAE.—In this family the external mycelium in some genera is slender as in the preceding family, but is constricted at more or less regular intervals. The constrictions are sometimes plugged by granules of carbohydrate nature to which the name

cellulin has been given. Similar granules are found scattered in the cytoplasm as well. The cell walls give the cellulose reaction immediately when treated with chloriodide of zinc or with iodine and sulphuric acid. In other genera a stout basal piece is produced just outside the substratum and from its apical portion arise the slender hyphae which bear the reproductive structures. These hyphae are mostly constricted regularly. All the known species of the family are saprophytic on matter of vegetable origin. Some species are aquatic growing chiefly on sticks, fruits, etc.; others grow unattached in water rich in organic matter; others grow in soil.

The oogones differ from those of the Family Saprolegniaceae in that the single egg is surrounded by a layer of protoplasm called the periplasm, while in the Saprolegniaceae the eggs, whether single or numerous, lie in the otherwise empty oogone. Five or six genera are recognized.

Leptomit, of which *L. lacteus* (Figure 28, *H*) is perhaps the only species, consists of branching, cylindrical hyphae about uniform in size, found in water containing large amounts of organic matter, such as drainage water from sugar factories, near the mouths of sewers, etc. It is easily distinguished by its constrictions which may remain open or become plugged by granules of cellulin. The terminal segments first and then successively the segments behind these become converted into zoosporangia in which are produced numerous pear-shaped primary zoospores which may all escape successively through the terminal zoosporangium or may escape from separate openings from each zoosporangium. The zoospores act as do those of *Saprolegnia*, eventually giving rise to zoospores of the secondary type. Sexual reproduction is unknown.

Sapromyces, with two or more species, grows on sticks, etc., in water, being attached by the rather few rhizoids. The upright main axis is not much thickened as compared with the several slender, constricted branches that arise at its apex. These bear at their apices, one to several obovoid clavate or cylindrical zoosporangia which give rise to numerous biflagellate, kidney-shaped zoospores which escape directly or into an evanescent vesicle. Possibly due to sympodial growth some of the zoosporangia may seem to be lateral. On the same branches with the zoosporangia or on separate branches arise the oogones and antherids. These may also be in terminal clusters of two or more, or single, or may appear to be

lateral. The obovoid oogones contain each a single egg with abundant periplasm. The clavate antherid is borne on a slender, sometimes coiled hypha, arising just below the point of attachment of the oogone. It is attached to the apex of the oogone.

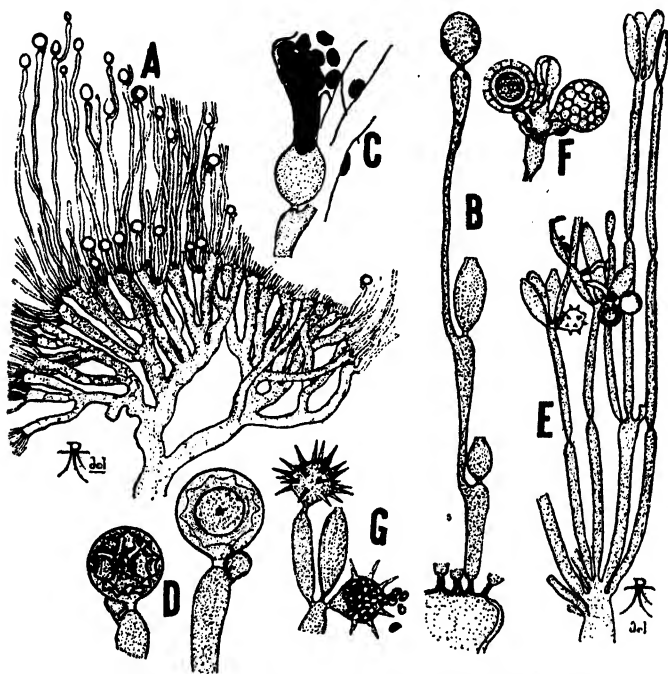


FIG. 29.—Saprolegniales. A, *Rhipidium americanum*, habit sketch; B, branch bearing two emptied and one immature zoosporangium; C, discharge of zoospores; D, oogone with mature oospore and antherid; E, *Araispora pulchra*, upper portion of plant bearing ordinary and spinose zoosporangia and sexual organs; F, oogones and antherids; G, ordinary and spiny zoosporangia. (After Thaxter, 1896.)

Rhipidium (Figure 29, A-D) with four species consists of a thick, more or less cylindrical body with numerous rhizoids, growing on fruits, twigs, etc., in water. At its top it gives off slender branches which are constricted here and there. Terminally on these branches arise the ovoid zoosporangia which may later appear lateral on account of the sympodial mode of growth of the hypha. The protoplasmic contents of the zoosporangium divide into numerous zoospores which push out into a cylindrical vesicle. Upon the rupture of the latter the biflagellate kidney-shaped zoospores escape.

The oogones are also terminal on slender branches and contain each a single egg surrounded by a layer of periplasm. The antherid may arise on a short slender branch just below the oogone or on a larger branch from another plant. It attaches itself to the basal portion of the oogone (Figure 29, *D*). The oospore is thick-walled and roughened areolately. The manner of germination of the oospore has not been reported.

Araiospora (Figure 29, *E-G*), with two or three species, grows like *Rhipidium* on vegetable matter in water. It has a thick supporting or storage body from which arise the numerous slender constricted branches bearing the reproductive organs. The zoosporangia are of two kinds, ovoid or club-shaped with smooth walls, and sub-spherical and covered with stout spines (Figure 29, *G*). The zoospores are similar in each type, being biflagellate and kidney-shaped. On similar branches, sometimes on distinct plants, are borne the spherical oogones. These are characterized by a cellular appearance caused by the manner of vacuolization of the periplasm. The oogone is fertilized by a basally applied antherid which may arise near by (Figure 29, *F*).

Two or three other genera are known but are rarely seen.

FAMILY ANCYLISTIDACEAE.—These organisms are parasitic in aquatic organisms, mostly algae, occasionally Nematodes, rarely in other plant tissues. Some species occur in pollen grains that have fallen into the water. They consist of short unbranched or shortly branched coenocytic tubes, usually confined to a single host cell, sometimes penetrating adjacent host cells by means of a slender germ tube. A biflagellate zoospore encysts externally on the host cell and sends a slender germ tube into the cell, enlarging when through the wall to form the above-described coenocytic mycelium. When mature this divides into several segments each of which may become a zoosporangium (Figure 30, *A*) or a sexual organ (Figure 30, *E*). Each segment has several nuclei. These increase in number in the zoosporangia and as many zoospores are formed as there are nuclei. These escape through slender exit tubes which penetrate the wall of the host cell. They may escape separately or may pass completely formed or imperfectly formed into a bladder-like vesicle (Figure 30, *B*) at the mouth of the exit tube, escaping by the rupture of the latter. They are biflagellate and kidney-shaped (except possibly *Achlyogeton* which was described in 1859

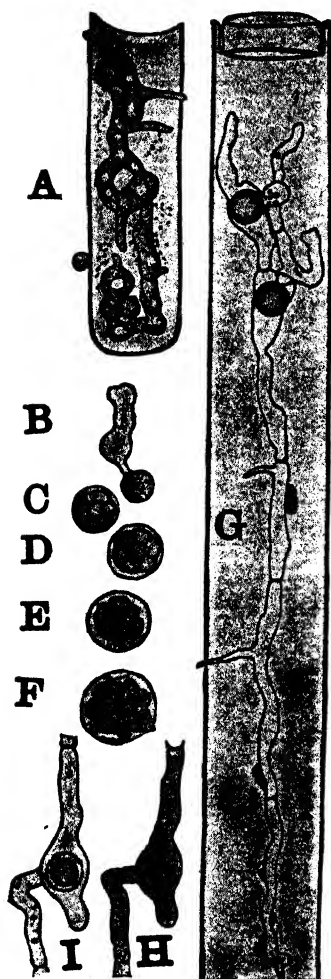


FIG. 30.—Saprolegniales, Ancylistidaceae. *Lagenidium rabenhorstii*. A, the coenocyte has divided into several zoosporangia; B, the protoplasm is escaping into a vesicle; C–F, stages in zoospore formation in the same vesicle; G, male and female plants in the host cell, the oogones containing mature oospores; H and I, two stages of fertilization of the same oogone. (After Zopf, 1885.)

as having uniflagellate zoospores but has not been studied for this point since). In one genus (*Ancylistes*) the zoospores are not produced but the zoosporangia send out slender germ tubes which seek out and infect other host cells.

In sexual reproduction adjacent segments in homothallic species or segments from adjacent plants in heterothallic species (Figure 30, G) function as antherids and oogones. In *Myzocyttium* the number of nuclei becomes reduced from 5 or 6 or more to 2 for the antherid and in the oogone finally becomes reduced to one. Through a beak-like process one nucleus passes from the antherid into the oogone where it finally fuses with the female nucleus. The resultant thick-walled oospore, lying free in the oogone, eventually forms a number of zoospores which escape by the rupture of the oospore wall. In *Ancylistes* the fusion of the sex nuclei has not been observed and the oospore germinates by a germ tube. The nuclear behavior of *Lagenidium* has not been investigated nor the manner of oospore germination.

These fungi are mostly found while studying the algae in which they parasitize, so that although apparently not rare their discovery is usually only incidental to other studies. Their microscopic size and the difficulty of maintaining the proper conditions for development on the microscope slide make the study of their life history difficult.

It must be noted that some species of *Pythium* (Order Peronosporales) which are parasitic within the filaments of fresh-water algae are sometimes rather reduced in size and show considerable resemblance to members of the Ancylistidaceae. Indeed, it has been suggested that possibly the latter are not properly placed in the Saprolegniales but belong, rather, in a position close to the Pythiaceae.

At this point it seems fitting to consider some of the theories as to the phylogeny of the foregoing groups. These theories fall into two classes, those in which the ancestry of the filamentous Phycomyceteae is sought in the Chytridiales and those in which the Siphonaceous algae are considered as ancestral forms. For many years the latter was the theory held by probably the majority of mycologists. In America the studies of Atkinson and Fitzpatrick and in Europe in recent years the investigations of Scherffel have focussed the attention upon the other theory. It is worthy of note that de Bary apparently considered the Chytridiales as primitive Phycomyceteae.

This theory in its at present more generally accepted form derives the Chytridiales from primitive, naked one-celled organisms related to the Rhizopoda. Two series are believed to have arisen, those families with uniflagellate swarm-spores and one family in which these are biflagellate (Woroninaceae). By the expansion of the rhizoids into a true mycelium it is believed that the two series of Chytridiales have given rise respectively to the Monoblepharidales (through the Cladochytriaceae) and the Saprolegniales (through the Ancylistidaceae). The structural similarities of these two orders are thus believed to be the result of parallel development. The similarity in structure to the Siphonales is considered to be merely a case of convergence, but not an indication of relationship. A variant of this theory derives the Chytridiales from green unicellular algae of the *Chlorococcum-Phyllobium-Chlorochytrium* series.

In the other theory greater weight is laid upon the similarity of the mycelium of the Saprolegniales and Monoblepharidales to the coenocytic, non-septate filaments of some of the Siphonophyceae, such as *Vaucheria*. The only essential difference is the lack of chlorophyll. Septa are lacking except where reproductive organs are produced or to wall off an injury. Growth in length is apical, not intercalary. The granular cytoplasm in which numerous nuclei are embedded shows more or less active streaming in the rather

broad filaments. The zoosporangia are usually terminal and the oogones and antherids are terminal on the main branches or on short lateral more or less specialized reproductive branches. The zoospores of the Siphonophyceae (except in *Vaucheria* and *Derbesia* in which compound zoospores or syncytia occur) are pear-shaped with two apical flagella and resemble closely the primary zoospores of the Saprolegniales. In *Vaucheria* as in the Monoblepharidales, the cellulose reaction of the cell wall is not apparent with iodine reagents (chloriodide of zinc or iodine and sulphuric acid) until after treatment with strong KOH solution. In the Vaucheriaceae the genus *Dichotomosiphon* as in some other families of the Siphonophyceae, has filaments regularly constricted like the mycelium of *Gonapodya* and *Allomyces* of the Monoblepharidales and of the Leptomitaceae in the Saprolegniales. The sero-diagnostic studies of Mez and his students indicate the closest possible relationship between *Vaucheria* and the Saprolegniales. It is still a much disputed point as to whether this is a valid method for determining relationships. If it is accepted as valid in other parts of the Vegetable Kingdom it would require strong contrary evidences to warrant considering it invalid here.

If the relationship of Siphonaceous algae and the Phycomyceteae is accepted then the two orders, Monoblepharidales and Saprolegniales may represent successive stages of evolution from a Siphonaceous form with both male and female gametes motile but unequal (as in *Codium* and some species of *Bryopsis*), through a form like *Allomyces*, then to *Monoblepharis*, with egg non-motile and only sperm motile, and finally to the condition found in all of the Saprolegniales, viz., fertilization of the egg through a conjugation tube growing out from the antherid. The difficulty with this hypothesis is that *Allomyces* and *Monoblepharis* have uniflagellate zoospores while the Siphonophyceae have biflagellate zoospores as do the Saprolegniales. Mez makes the suggestion that the latter have evolved from a point close to *Vaucheria* and that the *Monoblepharidales* have arisen from a point lower down in the Phylum Siphonophyceae where the gametes of both sexes are motile, thus making a diphyletic origin for the Class Phycomyceteae.

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CHAPTER IV

PHYCOMYCETAE. PERONOSPORALES

The more commonly observed and studied representatives of the **Order Peronosporales** are strict endoparasites within Flowering Plants (Anthophyta or Angiospermae). In order to understand their relationship it is necessary to study the fungi included in the Family Pythiaceae, a group intermediate between the Saprolegniales on the one hand and the typical Peronosporales on the other. The intermediate nature of this family may be shown by the fact that its typical genus *Pythium* has been assigned to the Saprolegniales by some authors and to the Peronosporales by others.

In general the Peronosporales are marked by the possession of a more slender mycelium than in the majority of the Saprolegniales. The species are either strict parasites or if saprophytic, in most cases at least, capable of parasitism in higher plants (several species of *Pythium* are parasitic on algae). These saprophytes or facultative parasites are mostly soil inhabitants. In most cases (except in the transitional species of *Pythium* with filamentous sporangia) the sporangia are enlarged and mostly separable from the mycelium as "conidia." The zoospores when formed are always of the secondary type, kidney shaped with two lateral flagella. Sexual reproduction, as in the Leptomitaceae, is by the fertilization through a conjugation tube, of the single egg which is surrounded by periplasm, to form a thick-walled oospore.

Following Fitzpatrick the approximately 425 known species are divided into three families, as follows:

FAMILY PYTHIACEAE.—Saprophytic or parasitic, mycelium intracellular, less often intercellular with haustoria. Zoosporangia filamentous to ovoid or spherical, remaining attached to the mycelium when submerged, in some cases the ovoid forms becoming separable "conidia," if aerial. These "conidia" are borne singly or on a sympodially branched conidiophore. They germinate by the formation of zoospores or by a germ tube.

FAMILY ALBUGINACEAE.—Strictly parasitic in herbaceous Anthophyta (Angiospermae). Mycelium intercellular with globular haustoria. Conidiophores clavate, clustered in extensive sori under the epidermis of the host which is ruptured by the pressure of the conidia which are produced successively in chains at the apex of each conidiophore. Conidia germinating by the formation of zoospores or of germ tubes. Oospore germinating by the formation of zoospores.

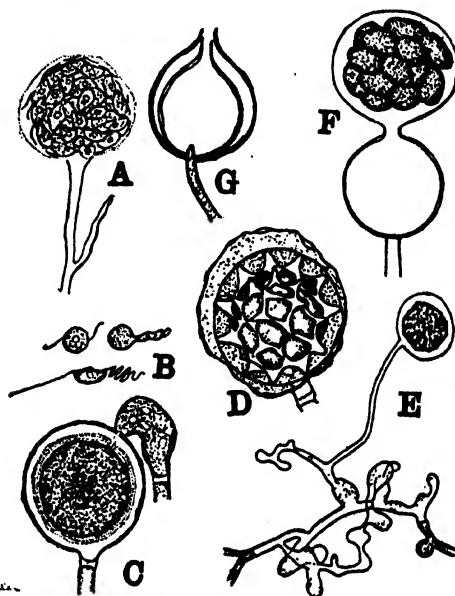
FAMILY PERONOSPORACEAE.—Strictly parasitic in herbaceous, and more rarely woody Anthophyta (Angiospermae). Mycelium intercellular with globular or filamentous haustoria. Conidiophores emerging through the stomata singly or two or three, unbranched or much branched, bearing the conidia singly at the tips of the branches or on short sterigmata on the unbranched conidiophore. Conidia germinating by the formation of zoospores or by a stout germ tube. Oospore germinating by germ tube or by a short unbranched conidiophore.

The PYTHIACEAE have been variously divided into from four to fourteen genera. Of these *Pythium* (in its wider delimitation) and *Phytophthora* contain the greater number of species and are best known.

The species of *Pythium* are mostly soil inhabitants, probably living most of the time as saprophytes. Some of these soil species and or ever, are capable of becoming destructive parasites upon the hyphae causing rotting of the tissues or damping off. A few may be apical *Pythium proliferum*, which can be caught by zoosporangia (arise bodies of water) are saprophytic upon vegetation (Figure 31, G), submerged in water, or even parasitic in a low point of attachment by Sparrow. The latter has been replaced by a new zoosporangium upon a marine species of the Florideae. *Achlya*. In some species land plants the mycelium is intracellular on aerial hyphae in which rapidly, in some cases appearing to be distributed by currents of arrival of the hyphae. water either in the usual manner

The mycelium is slender and, as carried detachable zoosporangia septate, branching coenocyte. In the submerged zoosporangia the mycelium are not noticeably other species they are somewhat has been studied by Trow, Pam, of the subgenus *Sphaerosporangium* been found to resemble zoosporangia representing potential conidia, is The spherical oospore arising off parasite of seedlings when the soil

longer or shorter unmodified hyphae. Of the several nuclei in the oogone all but one migrate to the periphery into the periplasm which surrounds the centrally-placed egg. The antherid is also plurinucleate and is terminal on a slender filament. Through a conjugation tube one male nucleus is introduced into the egg which then forms a thick wall and becomes an oospore. This may wait



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ary type, kidney shaped spores. A-D, *Pythium dictyosporum*. A, formation of zoosporangium; B, zoospores; C, young oogone and oospore; E, *P. torulosum*, toruloid zoosporangium and conjugation tube, of the single zoosporangium with vesicle; G, proliferated zoospore to form a thick-walled oospore (W, 1931; E-G after Matthews, 1931.)

Following Fitzpatrick the a germinating. Germination is effected by the divided into three families, as the be or of a short germ tube terminating

FAMILY PYTHIACEAE.—Saprophytic cases the oospore may produce the cellular, less often intercellular reproduction is mostly by means of filamentous to ovoid or spherical, zoosporangium forms a beak (usually when submerged, in some cases as long as the diameter of the separable "conidia," if aerial. These beak breaks open and out of it or on a sympodially branched conidiangium, to form a spherical by the formation of zoospores or by a germ tube (F). Within this vesicle

had already occurred in the zoosporangium, is completed and the kidney-shaped, biflagellate zoospores rupture the plasma membrane of the vesicle and escape singly or several in a clump, separating subsequently. The zoospore after swimming for a while encysts and germinates by a germ tube or, as observed by Sparrow, sends out a short papilla from whose apical opening emerges a single zoospore, with or without a vesicle, or sometimes a vesicle in which are produced several zoospores. The process may be repeated three or four times, the zoospores of the successive crops being smaller each time.

There are tremendous differences among the different groups of species as to the structure of the zoosporangium. In certain aquatic and soil forms (forming the subgenus *Aphragmium*) there is no septum setting off the zoosporangium from the remainder of the mycelium. The tips of several of the hyphal branches open (Figure 31, A) and the contents of the hyphae emerge to form vesicles within which zoospore formation proceeds in the usual way. The species of the subgenus *Aphragmium* are sometimes united with the subgenus *Nematosporangium* in which there is a septum which separates the otherwise similar zoosporangium (Figure 31, E) from the mycelium. This opens at one or more points to form vesicles. Schröter as well as Sideris raise this group to generic rank. In the subgenus *Sphaerosporangium* the zoosporangia are ovoid or spherical (Figure 31, F and G), single or catenulate at the hyphal tips, more rarely intercalary. The point of emission may be apical or lateral. In some submerged species new zoosporangia arise within the emptied zoosporangium by proliferation (Figure 31, G), as in *Saprolegnia*, or a branch arises just below the point of attachment of the zoosporangium and is terminated by a new zoosporangium, sympodial development as in *Achlya*. In some species some of the zoosporangia are produced on aërial hyphae in which case they may become detached and distributed by currents of air, germinating when they fall into water either in the usual manner or by a germ tube. Such wind-carried detachable zoosporangia are called conidia. In some species the submerged zoosporangia and the aërial conidia are alike, in other species they are somewhat different. *Pythium debaryanum*, of the subgenus *Sphaerosporangium*, with its zoosporangia representing potential conidia, is common in soil as a damping-off parasite of seedlings when the soil

is too moist or the seedlings too much crowded. It can often be obtained by placing a little soil in a dish with some cooled boiled water and placing in the latter a few (not too many or the bacteria will become too numerous) boiled hemp seeds. On these seeds the *Pythium* and various Saprolegniales will appear in a few days. *Pythium aphanidermatum*, the cause of black-root disease of radishes (especially noticeable in the White Icicle variety) and rotting of sugar-beet seedlings, is a species with slender hypha-like zoosporangia. It was originally described as the type of a new genus *Rheosporangium*, by Edson.

The genus *Phytophthora* contains some species that live as saprophytes in the soil, developing as parasites in the presence of suitable host plants. Other species are usually found as parasites on higher plants, although even these are capable of cultivation on non-living culture media. The zoosporangia of the soil-inhabiting types may be submerged and then remain attached to the mycelium, or may emerge into the air in which case they may become detached and are wind-distributed. In the more strictly parasitic forms the conidiophores emerge through the epidermis of the host, directly or through the stomata. They are simple or may branch sympodially. In all species the zoosporangium or the conidium when it falls into water may produce zoospores which emerge singly or pass out into a vesicle which soon ruptures so as to allow the escape of the zoospores. The latter resemble those of *Pythium* and are like the secondary zoospores of the Saprolegniales. These zoospores swim for a while and then encyst. They then germinate by a germ tube. The conidia instead of producing zoospores may produce short conidiophores upon which one or more smaller conidia arise or may germinate by a long germ tube. Sometimes the conidia germinate *in situ* without becoming detached.

As in *Pythium* the mycelium of many species is intracellular, directly killing the invaded cells, but in some species it seems to grow intercellularly, sending haustoria into the adjacent cells (Cooper and Porter, Szymanek, Klebahn, Butler). In general the species act as destructive parasites, killing the tissues very rapidly.

Sexual reproduction is essentially like that in *Pythium*, the single egg surrounded by periplasm being fertilized by a male nucleus which passes from the adhering antherid into the egg through a conjugation tube. The antherid may arise as a separate branch and become

attached to the oogone at any point. In some species the antherid appears to surround the base of the oogone. This has been interpreted as an antherid coiled around the hypha bearing the oogone

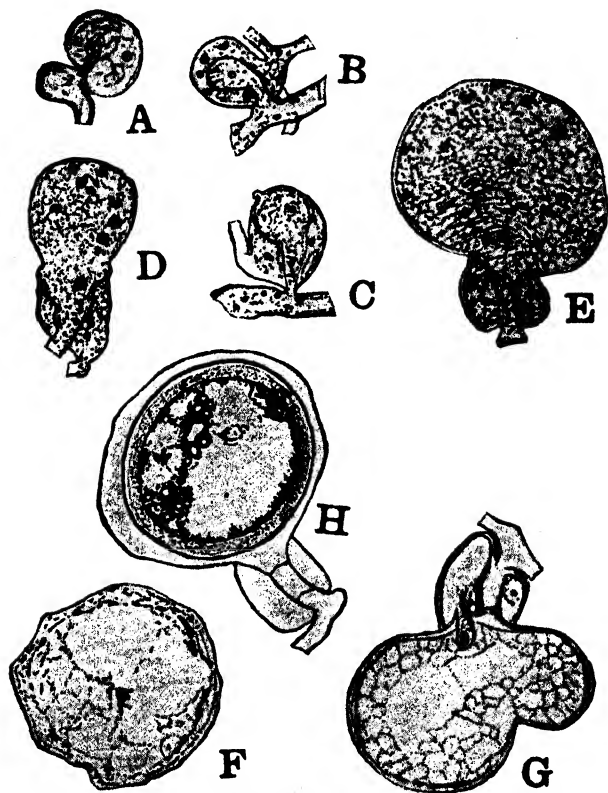


FIG. 32.—Peronosporales. *Phytophthora erythroseptica*, sexual reproduction with amphigynous antherid. A-D, stages in the penetration of the oogonial hypha through the antherid; E, oogone enlarging rapidly above the antherid; F, transverse section of oogone showing single egg nucleus at the center and supernumerary nuclei at margin of egg; G, fertilization of oogone, egg nucleus not visible because of angle of section; H, mature oospore with single zygote nucleus near center. (After Murphy, 1918.)

but Pethybridge seems to have proved that development is as follows (Figure 32): On the end of a hypha an antherid is formed and *through* this the supporting hypha grows, piercing the antherid completely and swelling then to form the oogone above it. In some species oogones may be found with these basal (amphigynous)

antherids and other with antherids in the usual position (paragynous). After fertilization the thick-walled oospore rests for some time and then germinates to form mycelium or a short conidiophore. Infection of the host may occur by the zoospores produced in the conidia or by the germ tubes from the oospores. With the soil inhabiting species the mycelium may directly penetrate the subterranean portions of the host. In some species, e.g. *P. infestans*, the mycelium overwinters in infected tubers which then give rise to diseased, spore-bearing shoots which serve as centers of infection.

Phytophthora infestans, the cause of the late blight of potato plants (*Solanum tuberosum*) and rot of potato tubers, was first observed as a serious enemy of this host about 1845. After being studied by various investigators it was first fully described by de Bary in 1876. For many decades oogone formation was unknown in this species until Clinton in 1911 reported their production in culture on oat agar. In 1927 Murphy reported finding them on the surface of tubers and in the surrounding soil. As in some other species these oospores were mostly parthenogenetic in origin although a basal antherid was observed in one case. In *Phytophthora phaseoli* Thaxter, the oogones were shown by Clinton to be produced in the seeds while the conidiophores cover the surface of the pods of the lima bean (*Phaseolus lunatus*). *P. cactorum* and some other species are troublesome rot-producing and damping-off fungi of many kinds of cultivated plants.

It must be noted that the border-line between some of the root-inhabiting species of *Phytophthora* and some of the conidium-producing species of *Pythium* is so vague that some mycologists, e.g. Fitzpatrick, have suggested uniting the two genera, which would then have to take the older name *Pythium*. Schröter, recognizing the similarity to the Saprolegniales placed *Pythium* in that group, but retained *Phytophthora* in the Peronosporales. This can not be upheld in view of the closeness of *Pythium* and *Phytophthora*. It merely goes to show the difficulty of drawing sharp delimiting lines in some cases. A number of other genera have been described in this family, some being soil saprophytes and others being serious parasites of various economic plants. By some mycologists they are merged with the genus *Phytophthora* and by other are maintained as distinct genera. Among these are *Pythiacystis*, causing the

brown rot of lemon, *Pythiomorpha*, aquatic and saprophytic, and *Trachysphaera*.

Albugo (1821) or as it is often called, *Cystopus* (1847), is the sole genus in the ALBUGINACEAE. The species number about twenty-five. In contrast with the members of the foregoing family the species are strictly parasitic, never occurring as saprophytes. They do not lend themselves to cultivation on culture media. Within some species (e.g. *A. candida*) there are numerous specialized races that are adapted to only certain host species or groups of species. The mycelium is strictly intercellular except for the small globular haustoria which are borne on the ends of short, very slender processes which penetrate the host cell wall. Melhus has shown that the mycelium of *A. candida* may overwinter in the tissues at or below the crown of such host plants as are winter annuals or biennials, growing out into the new shoots in the spring. The conidiophores (Figure 36, A) are formed on the ends of short, branched hyphae which arise from a mass of mycelium gathered in a limited area underneath the epidermis of the host (forming a sorus). They are club-shaped and stand, closely packed together, perpendicular to the surface of the epidermis, between it and the subepidermal cells. From the apex of each conidiophore are abstricted successively the spherical or ovoid plurinucleate conidia which are separated from each other by a slender connection, the disjuncter, whose dissolution permits the conidia to fall apart. The chains of conidia thus formed raise and eventually rupture the overlying epidermis, permitting the conidia to escape and to be distributed by air currents. The similarity of these sori, except for the color, to those of Rusts led to the name "White Rust" often applied to fungi of this genus. Upon falling into water the conidia divide internally into several uninucleate, biflagellate, kidney-shaped zoospores which escape by dissolution of a special spot in the conidial wall. After swimming for a short time these zoospores encyst and germinate by a germ tube. In some species Palm has shown that the conidia germinate usually by the production of a stout germ tube which infects the host without producing zoospores. Sexual reproduction takes place in the tissues of the host. Often the portions of the host plant in which this occurs are much hypertrophied. This is especially the case with *Albugo candida* in which the inflorescence and individual flowers of the host may be much thickened and enlarged. The distorted

flowers remain green and are sometimes several times as large as the normal flowers. On the ends of hyphal branches the almost spherical oogones are separated from the hyphae by septa. Stevens has studied the process of fertilization in several species. The oogone is at first multinucleate (Figure 33, *A*), the number of nuclei being

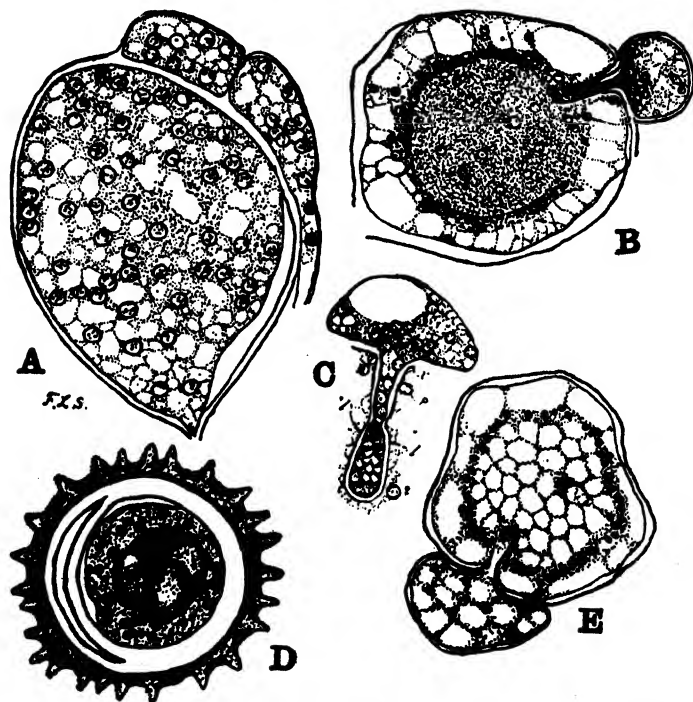


FIG. 33.—Peronosporales. *Albigo*, sexual reproduction. *A-D*, *Albigo bliti*. *A*, oogone and antherid before delimitation of the egg (oosphere); *B*, multinucleate egg ready for fertilization; *C*, antherid and multinucleate conjugation tube; *D*, mature oospore sectioned to show multinucleate condition; *E*, *A. portulacae*, showing single sperm and egg nuclei. (*A-D* after Stevens, 1899; *E* after Berlese, 1898.)

sometimes as high as 300. These may all pass to the periplasm leaving but a single egg nucleus in the egg (Figure 33, *E*) or after passing to the periplasm they may divide, half of the daughter nuclei remaining in the periplasm and the other half in the egg so that eventually the egg may contain about 100 nuclei (Figure 33, *B*). The multinucleate antherid on the end of a hyphal branch attaches itself to the oogone and eventually sends into the egg a conjugation

tube through which one male nucleus passes (Figure 33, E), in the first case mentioned above, or 100 or more in the second case (Figure 33, C). These male and female nuclei fuse by pairs. The fertilized egg produces a thick wall, consisting of a thin endospore and a thick, roughened episore. In the first type of fertilization the zygote nucleus divides repeatedly so that the oospore overwinters as a multinucleate structure (Figure 33, D). In the Spring zoospores are formed and the episore is ruptured, the endospore pushing out through the break as a bladder which in its turn ruptures and permits the zoospores to escape. Just where meiosis occurs is not yet certain. It has been suggested that the nuclear divisions occurring in the antherid and oogone before fertilization represent this process, or it may occur in the first nuclear division in the fertilized egg. In North America the common species are *A. candida* on various Crucifers (Brassicaceae); *A. portulacae* on purslane (*Portulaca oleracea*); *A. bliti*, on various species of *Amaranthus*; *A. tragopogonis*, on salsify (*Tragopogon porrifolius*) and other Composites; and *A. ipomoeae-panduranae*, on the sweet potato (*Ipomoea batatas*) and related plants. In most cases the disease caused is of minor importance.

The PERONOSPORACEAE like the Albuginaceae differ from the Pythiaceae in their strictly parasitic habit, the mycelium always being intercellular with haustoria penetrating the adjacent host cells. Like those of the Albuginaceae the haustoria of the Peronosporaceae may be knob-like but in many species they are filamentous or finger-like. The conidiophores of this family are external to the host and produce the conidia singly on the ends of the branches. As in Albuginaceae the conidia are plurinucleate. They germinate in most cases by the formation of zoospores, as in *Albugo* and *Phytophthora*. In *Peronospora* and *Bremia* the typical mode of germination is by means of a stout germ tube without the formation of zoospores. In *Rhyssolitea* (included in *Plasmopara* by many authors) the conidia germinate by the formation of zoospores (Figure 35), but in *Plasmopara* (in the narrower sense) the whole protoplasmic contents of the conidium escape as a naked plurinucleate but not flagellate mass which quickly rounds up and encysts and germinates by a germ tube. This difference in the mode of germination is the basis for Wilson's division of *Plasmopara* into the two genera. In nearly all, a very which germination by means of

zoospores is typical the conidia may, under special conditions germinate directly by germ tubes. A. de Bary, Melhus and others have shown that as in *Albugo candida* so also in this family, particularly in the genus *Peronospora*, the mycelium can live over winter in the tissues of a biennial, winter annual or perennial host and thus infest

the new plants in the spring without the aid of conidia or oospores. Sexual reproduction is like that in those species of *Albugo* in which the mature oogone contains a uninucleate egg (Figure 36, B, D). Mostly the oospore germinates by a stout germ tube or by a short conidiophore terminated by a single large conidium (as reported by Gregory in *Rhysoctheca viticola*, Figure 35), sometimes, as in *Albugo*, by the direct formation of zoospores.

The six or more genera of *Peronosporaceae* are mainly distinguished on the basis of their asexual characters. In the genus *Basidiophora*, with two species parasitic on Composites (Family *Asteraceae*) the conidiophore is club-shaped with its slightly swollen apex covered with numerous short sterigmata, each bearing a spherical conidium which produces zoospores when it germinates (Figure 36, B).

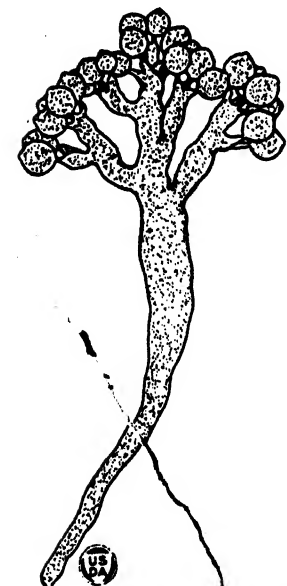


FIG. 34.—*Peronosporales*. *Sclerospora graminicola*, conidiophore. (After Weston, 1924.)

In *Sclerospora* the more or less dichotomously branched conidiophores are much thickened (Figure 34). The conidia germinate typically by zoospores. The oogone is grown fast to the oospore, the only genus in the family in which this occurs. The thirteen or more species are chiefly parasites of grasses (Family *Poaceae*). In the East Indies they cause serious injury to sugar cane (*Saccharum officinarum*) and to Indian corn or maize (*Zea mays*). *Sclerospora graminicola* is found frequently throughout the north temperate regions on fox-tail grasses (*Setaria* or *Chaetochloa*). The conidiophores form a downy layer on the under side of the infected leaves early in the morning but quickly dry down as the air becomes warmer and drier. After the oospores develop the leaves die and

shred longitudinally into thread like strips on which the oospores may be seen readily by the aid of a hand lens. Weston has given various species of this genus very careful study.

Plasmopara and *Rhysotheca* (Figure 36, C), usually united under the former name, produce slender, much branched conidiophores whose branches arise nearly at right angles. The tips of the branches

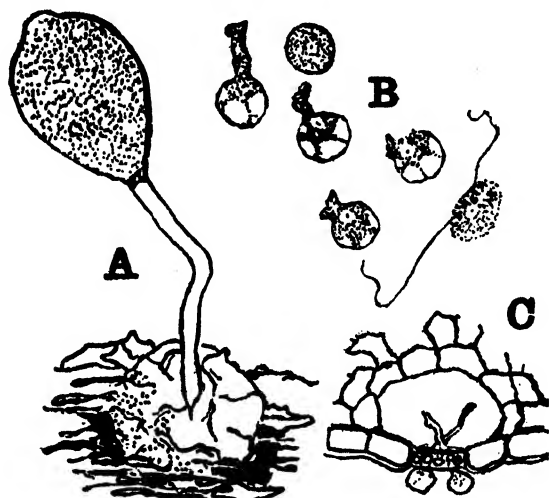


FIG. 35.—Peronosporales. *Rhysotheca (Plasmopara) viticola*. A, germination of oospore; B, zoospores active and encysted, and germination of the latter; C, infection of host tissue through stoma. (After Gregory, 1912.)

are truncate. The two genera differ, as mentioned above, by the mode of germination of the conidia, by zoospores in *Rhysotheca* and by a single naked mass in *Plasmopara*. The most important species from the economic standpoint is *Rhysotheca viticola* which causes the downy mildew and brown-rot of the grape foliage and fruit respectively (various species of *Vitis*).

Pseudoperonospora (called *Peronoplasmopara* by Clinton and others although the former name has priority) has slender conidiophores branching at acute angles and with pointed tips. The usually violet-tinged conidia germinate by zoospores. *Pseudoperonospora cubensis*, first described from Cuba, is probably native to Russia where its destructive effects have been known for years many years although the fungus was first recognized there in the p Rostowzew. It is a very serious enemy of the cucumber

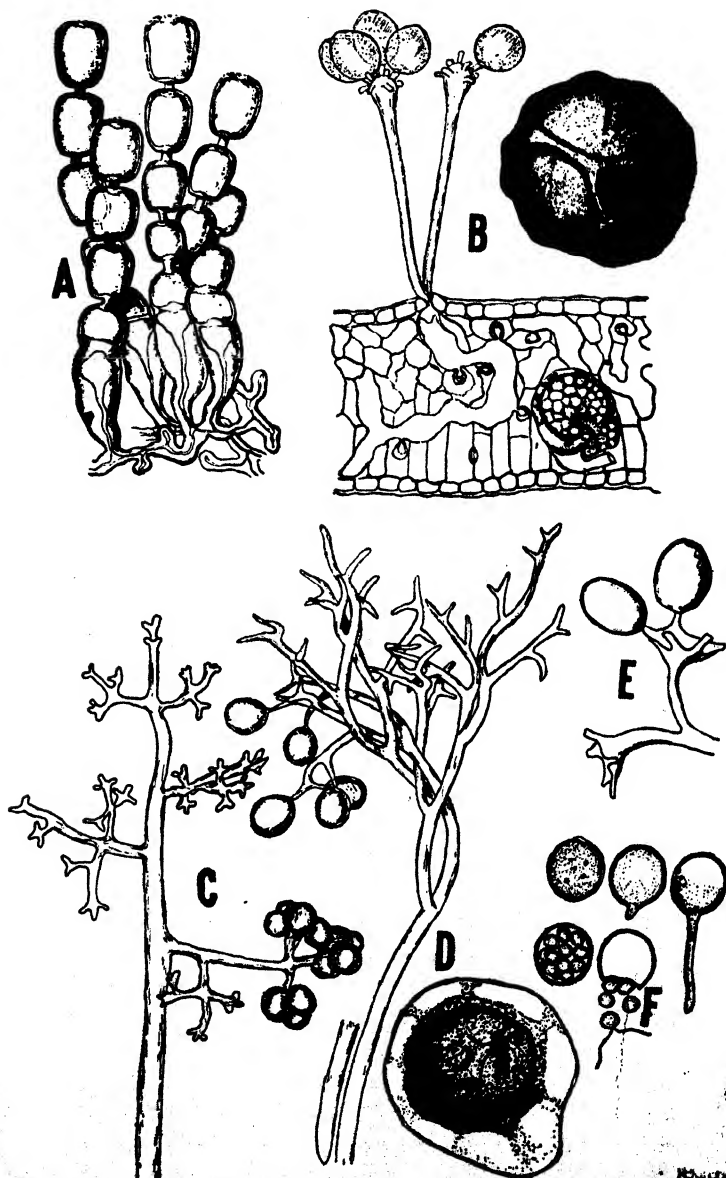


FIG. 36.—Peronosporales. A, *Albugo portulacae*; B, *Basidiophora edulis*; C, *Rhysotheca australis*; D, *Peronospora ficariae*; E, *Bremia lactucae*; F, *B. lactucae*, germination of conidia. (A–E after 1898; F after Milbrath, in Jour. Agr. Res., 1923.)

(*Cucumis sativus*) and muskmelon (*C. melo*). Another species, *Ps. celtidis*, attacks the hackberry (*Celtis*) while other species are found on hemp and on hops.

Bremia and *Peronospora* have slender conidiophores, branching at acute angles in a more or less dichotomous manner. Their conidia germinate typically by germ tubes, although zoospore production also has been reported for *Bremia* by Milbrath (Figure 36, *F*) and for one species of *Peronospora* (by Eriksson). In *Bremia* the tips of the branches enlarge into disc-like structures bearing sterigmata on their edges (Figure 36, *E*). *Bremia lactucae* is sometimes destructive to lettuce grown under glass. In *Peronospora* (Figure 36, *D*) the tips of the branches taper to a point. Gäumann recognizes 268 species in this genus. In but few cases are they of economic importance. *Peronospora spinaciae* is sometimes destructive in plantings of spinach (*Spinacia oleracea*) and *P. parasitica* on various Crucifers (Brassicaceae).

Gäumann, Wartenweiler and others have shown that the earlier recognized species of this family are separable by biometric and cultural means into large numbers of closely related species confined to very limited numbers of host species and differing constantly, but only slightly, in size and shape of the conidia and conidiophores. When such studies have been extended to all parts of the world and to all the forms occurring on different host species the number of species of Peronosporaceae will doubtless be very greatly increased.

Several other genera have been described which may be found to be justified. The physiology of conidial germination must be studied carefully in these as well as in the older genera. Only after such studies can we be certain that some of the generic distinctions now maintained or recently proposed are really valid. Should zoospore formation in *Peronospora* be confirmed it would seriously weaken the distinction between that genus and *Pseudoperonospora*.

The evolutionary tendencies within the Peronosporales are of interest to students of phylogeny. The species of *Pythium* with long narrow hypha-like zoosporangia would undoubtedly be included in the Saprolegniales were it not for those other species of *Pythium* with ovoid or spherical zoosporangia which may even function as separable conidia, thus forming a transition to *Phytophthora*. This genus still shows in some species a close relationship to *Pythium*, in the production of submerged zoosporangia (conidia) and faculta-

tive saprophytic habit, while in other species with well developed conidiophores and strictly parasitic habit the genus approaches closely the Peronosporaceae. The fact that the single egg in the oogone is surrounded by periplasm, as in the Leptomitaceae in the Saprolegniales, would suggest that the relationship of the Pythiaceae is closer to this family than to the Saprolegniaceae in which there is no periplasm and the majority of species have numerous eggs in the oogone. It has been suggested by some mycologists that from the Pythiaceae have been derived on the one hand the Saprolegniales (through the Leptomitaceae) and on the other hand the remainder of the Peronosporales. The very slender mycelium and more pronounced parasitic habit of the Pythiaceae would, in the author's opinion, point rather to their derivation from prevailingly saprophytic forms with coarser mycelium like the Saprolegniales. As obligate parasitism became prevalent in the Peronosporales evolution appears to have proceeded in several lines. The catenulate conidia of *Albugo* call to mind the proliferating zoosporangia of some species of *Pythium* as well as of *Saprolegnia*, while the sympodial conidiophores of the more advanced species of *Phytophthora* remind one of the sympodial branching in *Achlya* and some species of *Pythium*. The monopodial conidiophores of the Peronosporaceae do not resemble so closely any structures in *Pythium*. As parasitism has progressed we also find the transition from attached zoosporangia to separable zoosporangia (conidia) leading finally to the conidium found in *Peronospora*, in which zoospore formation has been lost, although the plurinucleate condition persists.

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CHAPTER V

PHYCOMYCETEAEE: SUB-CLASS ZYGOMYCETEAEE; MUCORALES AND ENTOMOPHTHORALES

The Sub-class Oomyceteae, discussed in Chapters III and IV, differs in a number of important points from the Sub-class Zygomyceteae. The former are strongly anisogamous, the latter are mostly approximately isogamous; the cell walls of the former contain true cellulose, the latter, according to von Wettstein do not possess cellulose but contain chitin along with pectose compounds. However, Mangin reports true cellulose in young sporangia of Mucorales and Hopkins finds both cellulose and chitin in *Mucor rouxii*. In the Oomyceteae zoospores are typically formed as a means of asexual reproduction, although suppressed in several genera; in the Zygomyceteae they never occur but are replaced by the homologous aplanospores.

Two orders are usually recognized; Mucorales and Entomophthorales. They may be distinguished briefly as follows:

Mucorales.—Mycelium very extensive, non-septate or septate in older aërial hyphae. Asexual reproduction typically by aplanospores formed in terminal sporangia. In a few genera these are reduced to indehiscent sporangia which function as conidia. Sexual reproduction usually present.

Entomophthorales.—Mycelium not very extensive, at first coenocytic but sooner or later becoming septate or falling apart into hyphal bodies. Asexual reproduction typically by conidia which are usually shot off with violence. Sexual reproduction frequently replaced by the parthenogenetic development of "azygospores."

The **Mucorales** are widely distributed fungi with a stout, well-developed, much branched, coenocytic mycelium, very similar to that of some representatives of the Oomyceteae. In the older mycelium, especially in the aërial portions, septa may divide it into plurinucleate segments, but the young mycelium and that submerged in the substratum usually remain non-septate. Asexual

reproduction is typically by the formation of non-motile, encysted spores (aplanospores) in sporangia terminal to the hyphae (Figure 37). These sporangia are formed in the same manner as in the three preceding orders, by the passage of a large portion of the contents

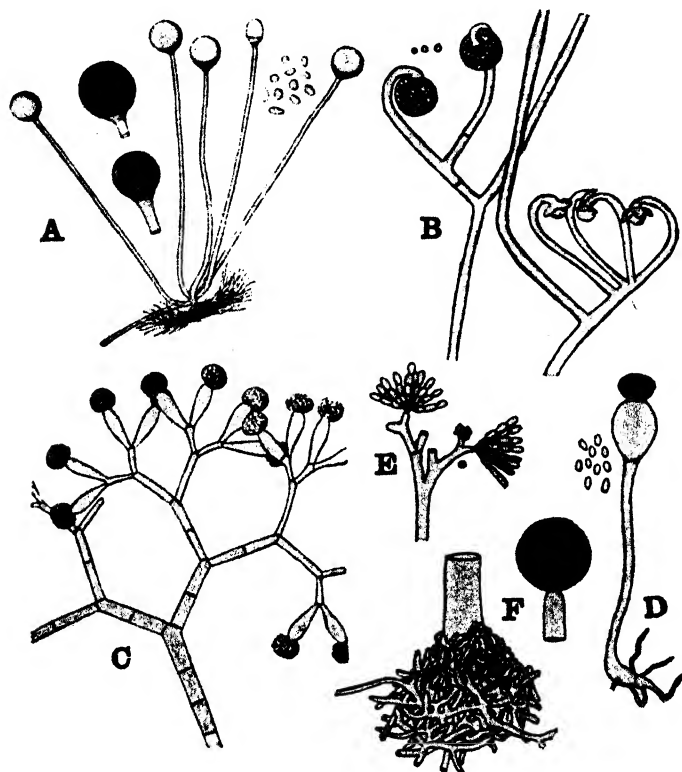


FIG. 37.—Mucorales. Asexual reproduction. A, *Rhizopus nigricans*; B, *Circinella minor*; C, *Sporodinia grandis*; D, *Pilobolus crystallinus*; E, *Piptocephalis freseniana*; F, *Mortierella rostafinskii*. (A and F after Brefeld, 1891; D after Brefeld, 1881; E after Brefeld, 1872; B and C after Lendner, 1908.)

of the hypha into a terminal enlargement which is then cut off from the hypha by a septum. The multinuclear contents of the sporangium are divided by cleavage planes into naked, at first polyhedral cells containing one or more nuclei, each. These then round up and encyst and escape by the rupture or dissolution of the sporangium wall. They germinate by a stout germ tube. Swingle has shown

that the contents of the multinucleate sporangium divide by cleavage of the cytoplasm into spores containing 1 to 3 nuclei, all of the protoplasm being used up in the formation of the spores. There are very interesting evolutionary modifications of this typical sporangium, leading to the development of structures comparable to conidia. Sexual reproduction (Figure 38) is typically by the union of two approximately equal gametangia to form a so-called zygospore which usually occupies the cavities of the two gametangia and develops thick walls. The gametangia are multinucleate. It is uncertain for most species whether many pairs of nuclei unite in the zygospore or whether the nuclei become reduced to only one pair. As in *Albugo*, both methods occur in this order. The zygospores germinate, usually after considerable time, by the formation of a germ tube which may become branching and start new mycelium or which may remain unbranched and terminate in a sporangium (Figure 38, B).

The greater part of the mycelium may be represented by that within the substratum, the aërial portion consisting of rarely more than that giving rise to the sporangia. On the other hand in many species the aërial mycelium may be very extensive, forming a large cottony mass from which arise, here and there, the sporangiophores. It is usually white but often the sporangiophores are dark colored. As it grows older this aërial mycelium may become septate but not truly cellular for the segments formed are plurinucleate coenocytes. A number of species of *Mucor* when growing in a medium rich in nutrients and of rather high osmotic pressure (e.g. a rather concentrated sugary medium) form a yeast-like growth instead of the normal filamentous mycelium.

The Mucorales are mainly saprophytic on vegetable matter, more rarely on animal matter, and are abundant in the soil and on plant debris. Some are weak parasites on still living plant tissues which are rich in stored food and rather inactive, such as the roots of the sweet potato (*Ipomoea batatas*). A number of species are parasitic upon other fungi, even upon other Mucorales. A few have been described as parasites on animal tissues.

The probable course of sporangial evolution within the Order Mucorales can best be followed by studying the sporangia of a selected list of genera. The genera chosen may not represent direct lines of descent, since the sexual reproduction is left unconsidered,

but they probably indicate in general the directions that the modifications followed.

The simplest and probably the most primitive type of sporangium is that found in the genus *Mortierella* (Figure 37, *F*). It must not be understood that this genus is considered as the most primitive of the Mucorales, for in its sexual reproduction it is so much modified from the more typical representatives of the order that it is clearly to be considered as well advanced in evolution. However, in its sporangial development it seems to have retained a very primitive structure. This is merely one of very many cases where evolution has advanced far along certain lines of development (in this case the manner of sexual reproduction) while remaining at about a standstill in other characteristics (asexual reproduction). The sporangium is a spherical enlargement of the apex of the sporangiophore, set off from the latter by a cross wall at the point where the enlargement begins. In sporangial evolution the next step appears to have been the development of a "columella." This in reality represents a displacement of the septum separating the sporangium from the sporangiophore so that it occupies a position arching up into the sporangium (Figure 37, *A*). This gives a much larger surface to the septum and permits a much freer transfer of food into the sporangium. Accompanying this more efficient food supply we find the sporangia to be larger, almost in proportion as the columella increases in size. In these two types of sporangium the numerous spores escape by the dissolution or breaking up of the relatively thin sporangial wall. The columella often remains firm and unchanged after the sporangium has ruptured and the spores have been set free. The sporangium of *Pilobolus* (Figure 37, *D*) represents a special modification of the foregoing type. In it the apical wall of the many-spored sporangium is very much thickened. The columella is rather small. Below the sporangium the sporangiophore is enlarged into a subsporangial vesicle that may be two or three times the diameter of the somewhat flattened sporangium. The sporangiophore tip is sensitive to light and this leads to the curvature of its lower part so that the sporangium is directed toward the source of the light. As the vesicle enlarges the turgor finally reaches such a degree that its apex ruptures and the sporangium is blown off, along with the watery contents of the vesicle, sometimes to a distance of several decimeters. The sporangia adhere to vegetation and are eaten by herbivorous

animals through whose digestive tracts they must pass before the spores are capable of germination. On the dung of these animals this mold grows and produces its conspicuous fructifications.

Returning to the genus *Mucor* we find that some species have unbranched sporangiophores while in others the sporangiophores may branch sympodially or monopodially, each branch terminating in a sporangium. Usually these sporangia are approximately equal in size although frequently the terminal one is slightly larger. In *Thamnidium* the terminal sporangium, which is often the first one formed, is larger and possesses a well-developed columella; somewhat below it there grow out from the sporangiophore short, often dichotomously much forked, branches all terminating in small sporangia or some in pointed spines. These small sporangia (sporangioles) are few-spored, sometimes with not over two to three spores, and possess no columella. The whole sporangiole becomes detached and distributed by air currents. As water is absorbed the spores swell and burst the sporangiole wall and escape. In some species of *Thamnidium*, under certain conditions only the sporangioles are formed. In the genus *Dicranophora* the sporangioles are only 1 to 2 spored and their spores are much larger than those in the terminal sporangium, which is often lacking. In *Chaetocladium* the large terminal sporangium is entirely lacking. The sporangioles are 1-spored and may be indehiscent in some species or in other species permit the spore to escape on germination. These monosporous sporangioles are often called conidia.

In *Blakeslea* the sporangium has a large columella (Figure 40, *I*) when the fungus is well-nourished and is smaller and few spored without a columella when poorly nourished. In addition numerous small two to four spored sporangioles (Figure 40, *H*) are formed on short sterigmata from the surface of the enlarged rounded heads clustered at the apex of a sporangiophore. These spores differ markedly in size and shape from those produced in the sporangia. In *Choanephora* the sporangium (Figure 40, *D*) possesses a columella and the sporangioles (Figures 40, *A*, *B*) are borne as in *Blakeslea* on round heads at the apex of the sporangiophore of the other type. They are monosporous and indehiscent and function, as in *Chaetocladium*, as conidia. In *Cunninghamella* the sporangia are never found and only the heads of indehiscent sporangioles ("conidia") are developed.

A further direction of sporangial modification is found in the Piptocephalidaceae. In this family the sporangiophores or their branchlets are somewhat swollen terminally and from these swollen portions there grow out radially numerous cylindrical sporangia (Figure 37, *E*). In these the spores are formed in a single row, the number ranging from 2 to 6 or 8 or more, rarely up to 12. As the spores approach maturity they may enlarge so that the sporangia are constricted between them and break apart into 1-spored pieces or the whole sporangium becomes detached and the spores escape one by one from the open base. In the former case the earlier students of these forms interpreted the structure as a chain of conidia.

A study of the sexual reproduction of the Mucorales reveals an interesting state of affairs. In perhaps the majority of species tested in this respect a culture started from a single spore as well as all cultures derived from sporangia produced on this culture will, when grown separately or in contact with each other produce no zygospores. On bringing such cultures in contact with other cultures of the same species made from plants obtained in various places it is found that sometimes at the line of contact between two cultures very abundant zygospore formation occurs. On their part these other plants are self sterile or sterile when grown in contact with each other so far as sexual reproduction is concerned. Thus A. F. Blakeslee determined that for many species of Mucorales there are two sexes, each capable of almost indefinite perpetuation by means of the asexual spores, but producing zygospores only when the mycelium of the one sex came into contact with that of the other sex. He named this phenomenon heterothallism and called such molds heterothallic. In contrast to these he found many species in which zygospore production would occur, when the proper conditions of nutrition and environment were met, within the mycelium originating from a single spore. Such molds he called homothallic. The common bread mold, usually called *Rhizopus nigricans*, is a good example of a heterothallic mold while *Sporodinia grandis*, a mold frequently found on decaying mushrooms, particularly *Amanita*, *Leptota*, *Russula* and *Lactarius*, is homothallic. Since the majority of Mucorales do not exhibit noticeable difference in size in the uniting gametangia it is impossible, for most species, to decide which plant should be called male and which female. Satina and Blakeslee

have made chemical tests on the two sexual strains of several species and find different reactions which seem to indicate to which sex each strain belongs. Blakeslee and others have observed that the sexual differences show different degrees of intensity. A plant that is very strongly male will conjugate with plants of all degrees of femaleness

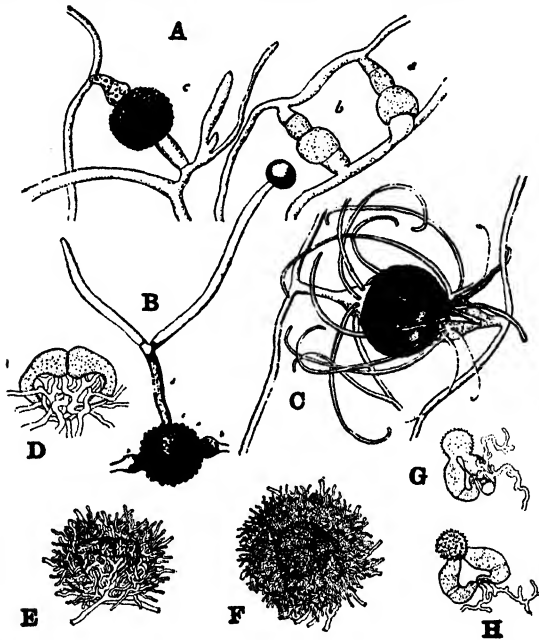


FIG. 38.—Mucorales. Sexual reproduction. A, a, b, c, *Mucor hiemalis*; B, *M. mucedo*, germinating zygospore; C, *Absidia glauca*; D-F, *Mortierella rostafinskii*; G-H, *Piptocephalis freseniana*. (A and C after Lendner, 1908; B, G, H, after Brefeld, 1872; D-F, after Brefeld, 1881.)

and vice-versa. On the contrary, a plant weakly male will not conjugate with one weakly female. Blakeslee has observed attempted conjugations between hyphae of different species or even genera, but only when opposite sexes were concerned. In this way it has been possible to correlate the sexes of the various genera and species of Mucorales. Burgeff has actually obtained hybrids between two species of *Phycomyces*.

The sexual process of the *Mucor* type is as follows (Figure 38, A-C): At a point where the hyphae come into contact (if of a heterothallic species these two hyphae must originate from plants of opposite sex) a swelling occurs on each hypha, pushing them

apart. The two swellings flatten against one another and become much enlarged, tapering down to the hyphae from which they arose. Soon a cross wall appears in each of these two processes, parallel to and a little distance from the flattened surface of contact, forming the two gametangia. The supporting parts are now called the suspensors. No significant differences in the size of the two gametangia can be noticed. Each contains a rather dense mass of cytoplasm with many nuclei. Beginning at the center the double wall separating the two gametangia dissolves away. In some cases there is a bulging of the central part of this double wall into one of the gametangia (from the male into the female gametangium?) before the wall is dissolved, and the cytoplasm and nuclei pass into this receptive gametangium. Soon, however, the whole intervening wall is dissolved away and the mingled cytoplasm fills out the cavities of the two gametangia. After the mingling of the cytoplasm most of the nuclei disintegrate leaving only a few privileged nuclei from each gametangium to unite in pairs. For *Sporodinia grandis* it has been shown by Lendner that only one pair of nuclei survives to unite and become the zygote nucleus. In *Phycomyces nitens*, on the other hand, Miss Keene has demonstrated that 6 to 8 pairs of privileged nuclei are left.

The density of the protoplast as well as the large number of granules of stored food make the study of the nuclear phenomena very difficult. The zygote begins to enlarge and the wall thickens, usually becoming warty or spiny externally. It is then called a zygospor. Germination generally does not occur until after a considerable time has elapsed. Usually a stout upright sporangio-phore is sent out after the outer wall of the zygospor has cracked open, and numerous spores are formed in a large sporangium. In the plant usually called *Mucor mucedo*, a heterothallic species, the spores produced in this sporangium are all of one sex, showing that the differentiation of the sexes must have occurred in some nuclear division within the zygospor prior to its germination. On the other hand in *Phycomyces nitens* spores of both sexes are found in the sporangium produced by the germinating zygospor, as well as, occasionally, a few spores that are not yet differentiated sexually and which produce homothallic plants. Even in these plants the spores in the sporangia that they bear become more and more differentiated into the two sexes. Evidently sexual differentia-

tion is delayed to a later stage in *Phycomyces* than in *Mucor mucedo*.

In a few species of Mucorales the gametangia and supporting suspensors are very unequal so that the product of the union of the two gametangia might be called an oospore. In general practice, however, they are called zygosporoes since their mode of origin is similar to that in isogamous species. In *Dicranophora* the one gametangium is many times larger than the other. In *Zygorhynchus* also, the difference between the two gametangia is marked. Both these genera are homothallic so far as this feature has been investigated.

In *Pilobolus*, *Mortierella*, *Piptocephalis*, *Phycomyces* and other forms the two sexual branches arise in contact and bend out and away (Figure 38, *D-H*), curving back so as to meet almost end to end, much as in a pair of tongs. In *Piptocephalis* (Figure 38, *H*) and *Endogone* (Figure 41, *I, J*) the zygosporoe does not form in the space occupied by the two gametangial cavities but buds out from these to form an external zygosporoe.

The zygosporoe remains naked in the majority of species. In *Phycomyces nitens* branches grow out from the suspensors, surrounding the zygosporoe loosely with stiff, black, more or less dichotomously branched processes. In *Absidia glauca* (Figure 38, *C*) these protective structures are curved and hooked. In *Mortierella* (Figure 38, *D-F*) they form a dense hyphal mass several layers in thickness, closely appressed to the zygosporoe.

The Order Mucorales is divided into several families. Mycologists are not in accord as to their number or limits. Probably these differences of opinion will remain well marked until greater agreement is attained as to the probable course of phylogenetic development within the order and as to the relative importance to be ascribed to the evolutionary processes involving the sporangia and those concerning the sexual processes. If the group is primitively isogametangic then the heterogametangic genera represent a later modification while if heterogamy is considered primitive then the isogametic condition found in *Mucor* is a modification of this heterogametic ancestral condition. The customarily used classification is based largely upon the sporangial structures and development and is probably artificial in many particulars. It can be replaced by a more natural system only when the above-mentioned questions

are settled satisfactorily. In this work eight families are recognized, following Fitzpatrick in the main.

FAMILY MUCORACEAE.—Sporangia relatively large and many-spored, oval or spherical, with a well developed columella. The sporangia are all alike and are borne singly, or several may be produced on a racemosely or otherwise branched sporangiophore. The most important genera are: *Mucor*, whose unbranched or branched sporangiophores arise from the main mycelium; *Sporodinia* (Figure 37, C), whose sporangiophores are repeatedly and closely dichotomously branched; *Rhizopus* (Figure 37, A), in which long stout creeping hyphae (stolons) form tufts of sporangiophores at the points where the stolons attach themselves by rhizoids. *Absidia* belongs in this family as do several other genera. The zygospores are naked or more or less protected and are produced by both the *Mucor* type and the *Pilobolus* type as described above. It should be noted that some of the names used above, e.g. *Mucor*, *Rhizopus* and *Sporodinia*, do not seem to conform to the rule requiring the earliest generic name (given not before 1753) to be used. By the strict application of that rule *Mucor* becomes *Hydrophora*, *Rhizopus* becomes *Mucor*, and *Sporodinia* becomes *Syzigites*.

FAMILY PILOBOLACEAE.—Sporangia flattened vertically with a thick, apical wall, in one genus the whole sporangium being shot away by the rupture of the apex of the swollen sporangiophore. The dung inhabiting species of *Pilobolus* are very easily obtained by bringing freshly dropped horse manure into the laboratory and enclosing it in a large dish. After a very few days the spores which have passed unharmed through the alimentary canal of the horse will produce an abundant growth of mycelium and the large, conspicuous sporangiophores will appear in large numbers. By enclosing the dish in a box closed on all sides except for a small window the sporangiophores can be induced to turn and discharge their sporangia in the direction of this window (Figure 39) without much scattering of aim, if the illumination is good. Miss R. F. Allen and Miss H. D. M. Jolivette and later Miss Jolivette studied the relation of the discharge to different colors of light qualitatively. Miss Parr studied these relations quantitatively. The light at the violet end of the spectrum is the most efficient, grading gradually to the red without intermediate maxima or minima. The presentation time, i.e. the minimum length of exposure necessary to bring about the effect, "varies

in inverse ratio to the square roots of the wave frequency" (Parr). Buller suggests that the enlarged apical region of the sporangiophore, immediately below the sporangium, may function as a light perceiving organ. Yet it must be noted that Miss Jolivet and Miss Parr both found the stage of greatest sensitivity to be that when the growing sporangiophore was pointed, before the tip had begun to expand.

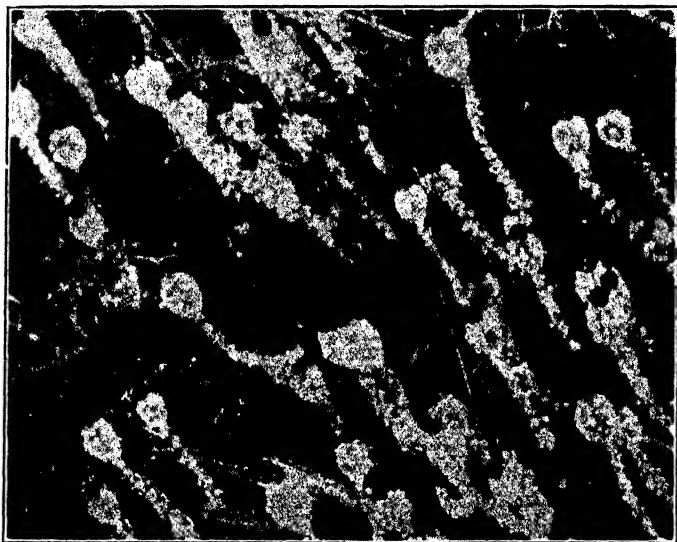


FIG. 39.—Mucorales. *Pilobolus* sp. showing growth toward the light. (Original, F. C. Strong.)

In this family the suspensors of the gametangia are curved like a pair of tongs.

FAMILY PIPTOCEPHALIDACEAE.—The species of this family are largely parasitic on other Mucorales although some are saprophytic. The sporangia are narrow and more or less clavate or cylindrical, with the spores usually in one row, appearing when mature like chains of conidia. Of the eight or ten genera *Piptocephalis* and *Syncephalis* are probably the best known. The sporangiophore of the latter, with its narrow, chain-like sporangia clustered on its swollen apex, resembles somewhat the conidiophore of *Aspergillus* with its clustered chains of conidia. The gametangia are formed as in *Pilobolus* but the zygosporangium buds out from the fused gametangia.

FAMILY THAMNIDIACEAE.—The genera of this family show the beginning of the differentiation into two types of sporangium, viz. the large terminal sporangium with a columella and the small lateral separable sporangioles which lack a columella. In *Thamnidium* the spores are alike in sporangium and sporangiole. In some species some of the branches upon which the sporangioles are borne are sterile and form spine-like processes. The zygosporoes are formed on approximately equal suspensors about as in *Mucor*. In *Dicranophora* the sporangioles are clasped by two or three finger-like processes at the apex of the branch. These fingers remain when the sporangioles are set free. The spores in the latter are very few in number and large and bean shaped, being small and ellipsoid in the sporangium. The gametangia are very unequal in size.

FAMILY CHAETOCLADIACEAE.—The single genus *Chaetocladium* is parasitic upon other Mucorales. It shows close relationship to *Thamnidium* both in its sexual reproduction, which resembles that in *Mucor*, and in the production of numerous sporangioles on forking branches some of which terminate in sterile spines as in *Th. fresenii*. The two genera differ in the complete absence of typical sporangia in *Chaetocladium* as well as in the fact that the sporangioles are monosporous and indehiscent, and hence are called conidia by many authors.

FAMILY CHOANEPHORACEAE.—The large sporangia are produced in two genera and possess a columella and resemble those of *Thamnidium*. The sporangioles instead of arising singly at the tips of forked branches are found crowded on the surface of the spherically swollen apex of a large sporangiophore. They are monosporous and indehiscent in two genera and several spored and dehiscent in one genus, *Blakeslea*. Most of the species are parasitic on flowers and other vegetable matter. Zygosporoe formation is essentially as in *Mucor*. *Blakeslea* possesses sporangia and several-spored sporangioles, *Choanephora* produces sporangia and indehiscent monosporous sporangioles, while *Cunninghamella* produces only the latter. Gäumann interprets the swollen apex of the sporangiophore as the homologue of the sporangium and the sporangioles clustered on its outer surface as in reality spores which have been as it were pushed out so as to become external instead of being produced internally. This view is not at all in accord with that of the author, who considers the sporangioles as homologous to

those of *Thamnidium*, i.e. reduced lateral sporangia. Possibly related to the foregoing is the genus *Mycotypha*, recently described by Miss Fenner. The mycelium is like that of most Mucorales, coenocytic and much branched and only occasionally septate.

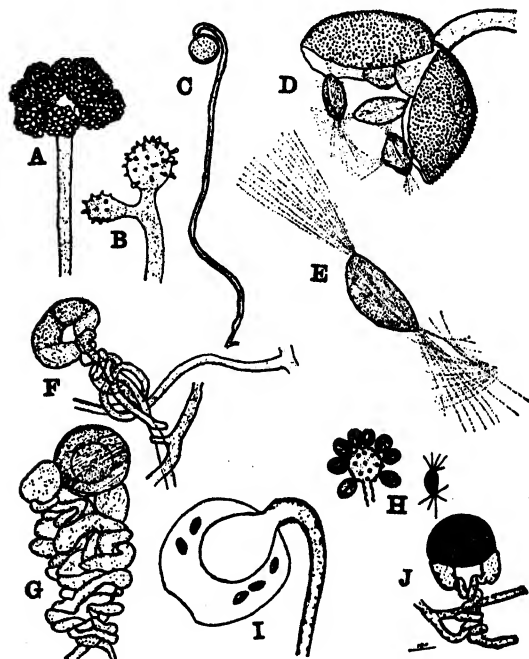


FIG. 40.—Mucorales, Choanephoraceae. A–G, *Choanephora conjuncta*. A, manner of bearing sporangioles ("conidia"); B, sporangiophore after the falling away of the sporangioles; C, sporangium; D, dehiscing sporangium; E, spore; F and G, stages in sexual reproduction; H–J, *Blakeslea trispora* H, head of sporangioles; I, large sporangium; J, zygospore. (A–G, after Couch, 1925; H–J after Weber and Wolf, 1927.)

The sporangioles are reduced to minute "conidia" closely covering the sides and apex of a cylindrical or clavate enlargement of the upper portion of the eventually septate sporangiophore. The resemblance of the head of sporangioles to the flowering head of *Typha* suggested the name given to the organism. So far the formation of zygospores has not been observed.

FAMILY MORTIERELLACEAE.—The position of this family is uncertain. In sporangial structure the absence of a columella would indicate a position below that of the Mucoraceae, but the occurrence

of sporangioles which are reduced to "conidia" in some forms would suggest a higher position. This is also indicated by the formation of a dense hyphal protective coat around the base of the sporangio-phore in some species and around the zygospores which are formed much as in *Pilobolus*. Of the several genera assigned to this family *Mortierella* is the only one that has been fairly well studied. In addition to the spherical, many-spored sporangia there occur in some species indehiscent, monosporous sporangioles ("conidia" or "stylospores"). The 30 or more species are mostly saprophytic on vegetable matter or weak parasites.

FAMILY ENDOGONACEAE.—The chief genus in this family is *Endogone* (Figure 41). The mycelium lives saprophytically in soil or in leaf mold. The reproductive structures are produced in loose or moderately firm, sclerotium-like bodies a few millimeters to two or three centimeters in diameter. These may contain either sporangia, chlamydospores or zygospores in large numbers, surrounded by a dense mass of hyphae. The zygospores occur as bud-like out-growths from the united gametangia, as in *Piptocephalis*. The suspensors lie almost parallel. In *Endogone fasciculata* the chlamydospores and the zygospores have been found in the same sporocarp. The sporangia are terminal on hyphae, separated from the latter by a transverse septum. The number of spores varies from 4 to 12 in some species and is very numerous in others. The spores are multinucleate, and are formed by cleavage of the whole protoplasmic contents of the sporangium. The sporangia and distantly septate hyphae are scattered throughout the sporocarp, some of them reaching the surface. Compound sporocarps occur, the separating layers being loose hyphae intermingled with humus material. All attempts so far to germinate the chlamydospores and zygospores have proved vain. Miss Walker has germinated the sporangiospores and grown the fungus in culture. The mycelium is coenocytic and shows frequent anastomoses. Cross walls are formed occasionally to wall off empty portions of the hyphae. The formation of the typical sporocarps could not be obtained. Until these fungi can be brought in culture to the stage of reproduction the connection of the various species of sporangial, chlamydosporic and zygosporic types can not be proved. About 19 species are recognized by Thaxter. In addition three genera producing only chlamydospores are ascribed to this family. Because of the sporangia with trans-

verse basal septum and of the zygosporangium involved in a complicated hyphal sporocarp it has been suggested that the relationship of this family lies most closely with the Mortierellaceae. Until the true nature of these fungi was elucidated by the investigations of Buch-

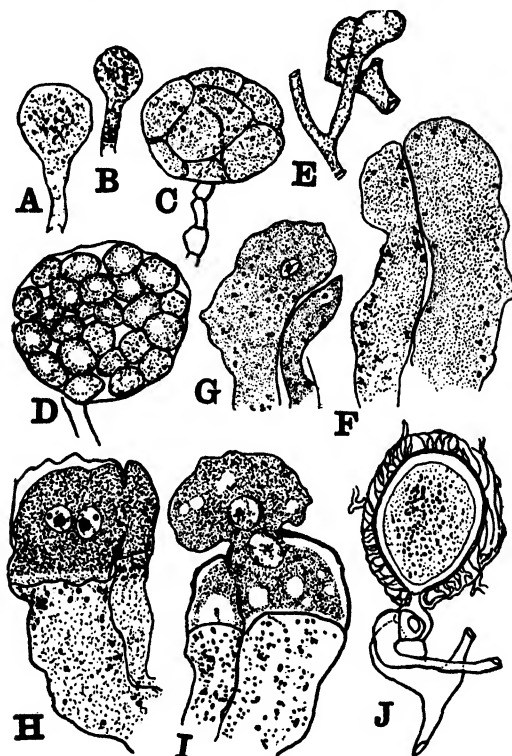


FIG. 41.—Mucorales, Endogonaceae. A-D, stages in the development of sporangia in *Endogone malleola*; E-J, stages in sexual reproduction of *E. lactiflua*. E, young gametangia; F, showing multinucleate condition in both young gametangia; G, a privileged nucleus enlarges in each gametangium and the other nuclei recede or degenerate; H, the male nucleus has passed through an opening into the female gametangium; I, the zygosporangium has begun to bud out of the female gametangium; J, almost mature zygosporangium. (A-D after Miss Walker, 1923; E-J after Bucholtz, 1912.)

oltz, Thaxter and Miss Walker they were assigned to positions among various other groups of fungi, being perhaps most generally considered to be forms of the Class Ascomyceteae.

The **Entomophthorales** are fungi whose mycelium is much reduced. Upon germination of the spore it is coenocytic but sooner

or later septa appear which divide it into plurinucleate or even uninucleate segments, forming a septate mycelium in some genera or in other genera falling apart into the so-called "hyphal bodies." These latter may multiply by fission. Of the five or more genera two are saprophytic (or rarely parasitic), one is parasitic in the gametophytes of ferns and the remainder are parasitic in the bodies of insects. The latter group includes the vast majority of the

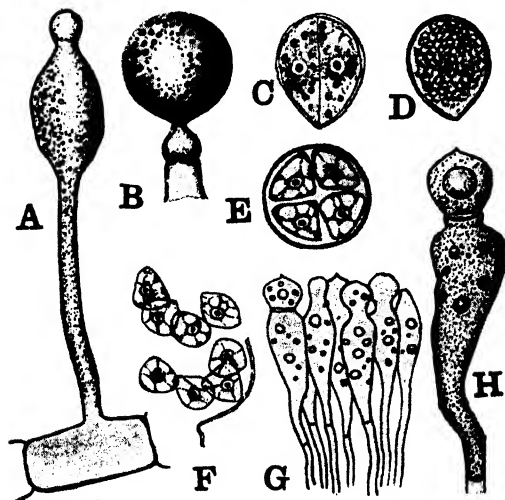


FIG. 42.—Entomophthorales, asexual reproduction. A-F, *Basidiobolus ranarum*. A, developing conidiophore; B, apex of mature conidiophore; C-F, development of "conidium" into sporangium in the stomach of frog; G, H, *Entomophthora muscae*, cluster of conidiophores and single conidiophore. (A-B and G-H after Thaxter, 1888; C-F after Levisohn, 1927.)

known species of the order. Asexual reproduction is by means of reduced sporangia (sporangioles) which may be uninucleate or plurinucleate and are shot off singly from the apex of a somewhat club-shaped sporangiophore, except in the genus *Massospora* in which they are produced internally in the body of the insect host. These sporangia are usually called conidia, as in the homologous structures in the Peronosporaceae and Mucorales. In many cases such a "conidium" may produce another "conidiophore" and shoot off a secondary conidium, and that may produce a tertiary conidium, and so on. The ultimate germination is by a germ tube except in the genus *Basidiobolus* in which the conidium shows its true sporangial nature by producing internal spores (Figure 42, C, D, E).

Sexual reproduction is by the union of mycelial segments (or of hyphal bodies) to form zygospores which may lie *in* one of the uniting gametangia (*Basidiobolus* Figure 43, C), *between* the suspensors (*Conidiobolus*) or laterally to the fusion cell or to one of the conjugating gametangia (*Entomophthora* Figure 43, F-K). The zygospore is thick-walled. In many species similar spores are formed partheno-

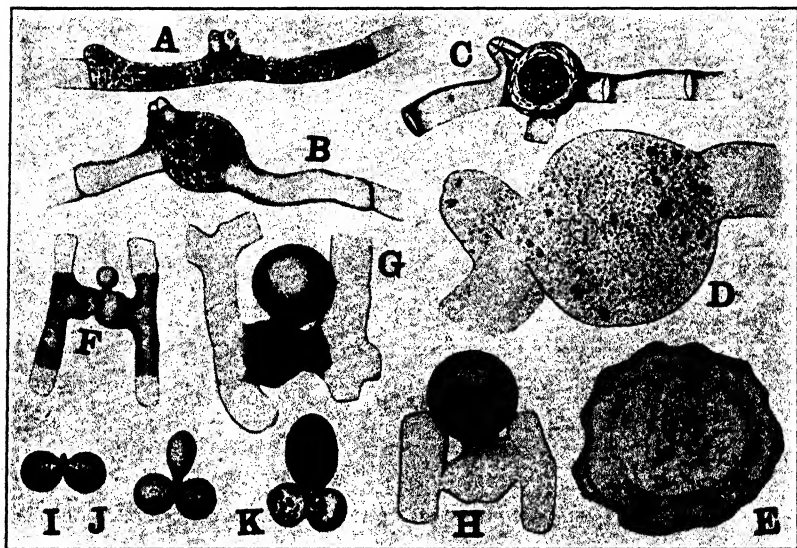


FIG. 43.—Entomophthorales, sexual reproduction. A-E, *Basidiobolus ranarum*; F-H, *Entomophthora sepulchralis*; I-K, *E. fresenii*, conjugation of hyphal bodies. (A-C after Eidam, 1886; D-E after Fairchild, 1897; F-K after Thaxter, 1888.)

genetically, the azygospores. Usually only one family is recognized, the Entomophthoraceae.

Conidiobolus is saprophytic or weakly parasitic on the fruit bodies of higher fungi. Its asexual spores are conidia, i.e. do not divide internally into sporangiospores. The zygospore is formed by the union of two unequal gametangia and as in most Mucorales occupies the cavities of the two uniting bodies.

Basidiobolus is saprophytic on the dung of frogs, lizards, etc. On the dung it forms sporangiophores (Figure 42, A, B) which shoot off the not yet divided sporangia much as occurs in *Pilobolus*. These sporangia are eaten by beetles which in turn are devoured by frogs or lizards in whose stomachs the beetles are digested, setting free

the sporangia which only then divide internally to produce the spores (Figure 42, C-F). These escape from the sporangium and multiply in the alimentary canal by fission or budding. They are set free in the excrement and then germinate to form mycelium on which are produced other sporangia. This mycelium is at first coenocytic but soon septa appear and divide it into a multiseptate, branched mycelium. Zygospor formation (Figure 43, A-E) is as follows: Two adjacent segments of a hypha send up parallel beaks in contact, into each of which a nucleus migrates and divides. One nucleus of each pair remains in the apex of its beak, being cut off by a septum. One of the two original segments enlarges considerably, an opening is dissolved through the separating septum and the nucleus and part of the cytoplasm of the smaller cell passes into the larger cell. There the nuclei fuse and a thick-walled "zygospor" is formed.

Completozia is parasitic in the cells of the gametophytes of ferns. Infection spreads from cell to cell of the host by means of hyphae penetrating the cell walls. Azygospores are formed in the host cells and conidiophores which emerge into the air and bear conidia which are violently discharged. The mycelial masses in the host cells are much branched and lobed and not conspicuously septate.

Entomophthora is the largest genus of this family, containing, according to Fitzpatrick, about 40 species, all parasitic within insects. This genus is known by some writers as *Empusa*, but since this name was used earlier for a genus of Orchids the next later name, *Entomophthora*, must be used. The internal organs of the host are dissolved, presumably by enzymes secreted by the fungus. The mycelium may be quite extensive and filamentous with only occasional septa or may become septate at frequent intervals or break apart into numerous hyphal bodies. The clavate conidiophores (Figure 42, G, H) pierce the thinner parts of the body wall of the insect and shoot off their conidia with great violence. The conidiophores may be simple and packed together in a palisade layer or they may be branched at the base. In the latter case the conidia are uninucleate; in the former they are plurinucleate. Both azygospores and zygospor (Figure 43, F-K) are known in this genus. It is not settled yet whether only one pair or several pairs of nuclei are functional, nor is it known at what stage of development of the zygospor the nuclei fuse.

Entomophthora muscae is the frequent cause of the death of house flies (*Musca domestica*) in the autumn months. The affected flies cling to window panes and other objects and die there, and the glass immediately surrounding them becomes whitened with a halo of discharged conidia. True zygospores are unknown but azygospores are produced abundantly in Europe but very rarely in America. *Entomophthora grylli* is very abundant in some seasons in the plains states of the United States, causing the death of immense numbers of grasshoppers which climb on stalks of grasses and other plants and there die. In moist weather their abdomens are at first covered by belts of conidiophores emerging from between the segments. In dry weather these are not conspicuous. Later azygospores are produced in great numbers in the body cavity of the host.

Several other genera have been described, including *Massospora*, parasitic in the seventeen-year cicada (*Tibicina septendecim*). In this genus the conidia are produced within the host, not on extruded conidiophores, and are distributed by the gradual sloughing off of the affected parts while the insect is still capable of creeping around. Sexual reproduction is unknown.

Recently Sawyer has devised means of growing species of *Entomophthora* in culture and has thus been able to follow out the life histories of some species more fully than formerly.

Leger has studied several forms which inhabit the aquatic larvae of insects and seem to belong to this order, but to distinct families, the Harpellaceae and the Genistellaceae. They form unbranched or branched tubes 100 to 700 μ long, at first uninucleate, later plurinucleate and eventually septate. On these are borne curved or boat-shaped conidia. By conjugation are formed zygospores which become uninucleate by the fusion of two nuclei. The uniting gametangia may arise from separate plants or from different branches of the same plant or even from adjacent cells of the same filament.

Undoubtedly the Entomophthorales have a close affinity to the Mucorales. They agree in their chitin-containing cell walls, in the production of zygospores (or azygospores), and in the formation of conidia which are closely homologous to the sporangioles. The different types of zygospore formation found in the Entomophthorales are also found in the Mucorales. It is impossible, without a clearer knowledge of the relationships within the latter group, to decide just at what point in this group the Entomophthorales arose.

Regarding the ancestry of the Zygomyceteae there is also great uncertainty. It is clear that the typical sporangia are homologous to the zoosporangia of the Monoblepharidales and Saprolegniales. The aplanospores can be considered as zoospores which have encysted within the zoosporangium as occurs in some genera of the Saprolegniaceae, e.g. *Geolegnia* and *Aplanes*. If the heterogamous genera of the Mucorales are the most primitive this would add to the probability that the latter are derived from some terrestrial Saprolegniaceous forms. On the other hand the genus *Zygochytrium* mentioned above in the discussion of the Cladochytriaceae has many characteristics that remind one of the Mucorales. The terminal zoosporangia are spherical and sexual reproduction includes the formation of a zygospore borne by two suspensors. This fungus needs further study having been observed only once, in 1874. The often made suggestion that the Mucorales are to be derived from the Order Zygnematales among the algae has little to commend it beyond the external similarity of the zygospores in both groups. The mycelium of the Mucorales is polyenergid, the filaments of Zygnematales are truly cellular; the sporangia of the former have no homologues in the latter; the multinucleate gametangia of Mucorales are entirely unlike the uninucleate cells which fuse to form the zygospore in the Zygnematales.

DOUBTFUL PHYCOMYCETEAE

The Order **Protomycetales**, with the single family PROTOMYCETACEAE, has long been the subject of speculation as to its true position among the fungi. The author follows Fitzpatrick in placing these fungi among the Phycomyceteae, but with considerable doubt as to the correctness of the assignment and with but very little idea as to what groups of that class may have given rise to these peculiar fungi. The more recent and extensive investigations on the group are those of Sappin-Trouffy and of von Büren. The family seems to have no affinity to the Ascomyceteae or to the other Higher Fungi, though it has been assigned to various positions among those fungi. It consists of one well established genus, *Protomyces*, with 12 or more species. Two other genera have been described, *Taphridium* and *Protomycopsis* but until life-history studies are more complete the validity of their segregation is uncertain. All the known species of

all three genera are parasitic in the stems, leaves or fruits of *Umbelliferae* and *Asteraceae* (*Compositae*) and *Cichoriaceae*. The mycelium is subepidermal or intercellular in the underlying tissues. It is septate at occasional intervals, each segment being several nucleate. The cell walls give a strong cellulose reaction with chloriodide of zinc. Some of the segments of the mycelium (only very rarely a terminal segment) enlarge and become multinucleate (30 to 40 nuclei, in *Protomyces inundatus*). Within the original cell wall the cell enlarges and becomes surrounded by a thick, three layered cellulose wall, the nuclei dividing several times to become 100 to 200 in number. This sporangium (or "chlamydospore" as some authors call it) may remain in the tissues over winter or may germinate the same season. They may, in some species, be subepidermal, or in others may be scattered at various depths. In germination the deeper lying sporangia produce their spores without breaking the exospore, while those lying nearer the surface of the host burst the exospore on that side and the contents bulge out like a balloon, still surrounded by the inner wall layer. The nuclei all migrate to the periphery and a large central vacuole is formed and by cleavage planes starting at the outside this thin layer of cytoplasm is divided into little uninucleate cells which divide twice (meiosis?) forming 4 ellipsoidal spores out of each cell. These spores now mass in the center of the sporangium and by the breaking of the latter are set free along with the slimy contents of the vacuole. Whether some unused cytoplasm ("epiplasm") is present is a disputed point. After being set free, sometimes before, the spores fuse by twos. Whether the nuclei unite is also disputed but von Büren's latest work seems to confirm the nuclear union. These fusion spores germinate to form yeast-like cells in culture or endophytic mycelium on the proper host.

The affinities of this family are exceedingly uncertain. The final division of the nuclei in the sporangium may be a reduction division. The cells that divide into 4 spores each have been called asci and the whole sporangium a "synascus" but the absence of nuclear fusion in these "asci" before the formation of the spores seems to exclude that possibility. The cellulose nature of the cell wall speaks for the *Phycomycetous* relationship. It has been suggested that they are related to the *Ancylistidaceae* or to the *Chytridiales* with loss of motility of the zoospores (or gametes).

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CHAPTER VI

THE HIGHER FUNGI: CARPOMYCETAEAE

INTRODUCTION

The fungi that have been the subjects of discussion in the foregoing chapters are frequently designated as the Lower Fungi in contrast to the often much more highly developed forms usually designated as the Higher Fungi. It may be well here to contrast the two groups as to their main points of difference, recognizing that though these distinctions are in general valid yet there are many forms of Higher Fungi in which these differences are not recognizable.

(1) The Phycomyceteae are prevailingly tubular coenocytes, non-septate except at regions of injury or where reproductive organs are cut off from the rest of the mycelium. (Exceptions may be noted in old aerial mycelium of some Mucorales and in most Entomophthorales.) The Higher Fungi are cellular, i.e. their hyphae are divided by septa into true cells, usually uninucleate or binucleate. (Exceptions are numerous. Thus old cells sometimes become multinucleate; on the other hand many young hyphae from germinating spores or young ascogenous hyphae may delay the formation of cross walls for some time. Aside from these, numerous species are scattered throughout the whole group in which almost all the cells are plurinucleate.)

(2) In the Lower Fungi sexual reproduction leads to the formation of a single, usually thick-walled, oospore or zygospore. In the Higher Fungi, wherever true sexual organs or processes can be distinguished, the union of sperm and egg or of cells substituted for these leads to the production of a many-celled structure, called by Sachs a "spore-fruit" all the cells of which may become the reproductive cells (as the ascospores in the asci of the Order Saccharomycetales) or of which only a part are reproductive cells, the remainder being necessary components of a more or less complicated fruit body (e.g. the sum of the ascogenous hyphae and asci arising from the oogone of *Pyronema*, along with the various hyphae of vegetative origin,

all of which form the apothecium, while only the ascospores are the reproductive cells).

(3) In the Phycomyceteae, except the Mucorales and the Entomophthorales, uniflagellate or biflagellate zoospores are generally produced as a means of asexual reproduction, while in the two orders just mentioned the asexual reproductive structures are clearly only modifications of zoosporangia. In the Higher Fungi the asexual reproductive cells are conidia, which are separable single cells (sometimes several-celled structures) of the mycelium with no indication of ever having had any homology with zoosporangia.

(4) The aquatic Phycomyceteae and the terrestrial Order Peronosporales have walls composed of cellulose (or carbohydrates closely related to cellulose). Cellulose is lacking in the Higher Fungi, or when present has been shown by Thomas to play only a subordinate part. In these the basis of the wall is chitin surrounded or mixed with carbohydrates and more or less fatty substances. Hopkins reports that neither chitin nor cellulose is present in several species of the Class Ascomyceteae and of the Class Basidiomyceteae, although other species of both classes tested by him showed chitin but not cellulose to be present, as is claimed by von Wettstein to be probably universal in these two classes. Senft reports that the ascogenous hyphae of *Chrysothrix nolitangere*, a lichen, respond to the standard cellulose tests. The Mucorales and Entomophthorales seem to occupy an intermediate position in that they have chitin in their cell walls and rarely have true cellulose, although other carbohydrates are present in the wall.

The Higher Fungi are with few exceptions terrestrial or epiphytic, a very few species are truly aquatic, some being parasitic upon marine seaweeds, but they possess none of the characteristics of a primary aquatic habit such as zoospores, etc. One order, the Laboulbeniales, consists exclusively of insect-infesting parasites. The remainder are mostly either saprophytes or parasites upon plants (exceptionally upon animals). All degrees of parasitism are found, varying from destructive parasitism, in which the tissues of the host are killed before the invading hyphae reach them (e.g. *Sclerotinia sclerotiorum*) to extreme cases of balanced parasitism (e.g. some of the Ustilaginales in which the fungus and host grow, together, for a long time with but little apparent harm to the latter). One large group has developed a special type of parasitism upon terrestrial or epiphytic freshwater

algae, forming peculiar structures which enclose the algal hosts. These are the Lichens. Some of the most harmful fungi from the economic standpoint, the Rusts and Smuts, are found among the Higher Fungi.

Asexual reproduction by means of conidia is widely distributed throughout the various classes and orders, but seems to be entirely lacking in some of the groups. The conidial production may consist only of the abstriction of a single cell from the tip of a short, unbranched conidiophore or the conidiophore may be longer and branched. The conidia may be produced successively at the tip, separating from the conidiophore as soon as formed or clinging together in a mucilaginous drop or remaining attached in a chain. A chain of conidia may produce new conidia acrogenously, i.e. each new conidium arises from the apical conidium of the chain, so that the basal conidium is the oldest and the apical conidium the last formed. This is the type of conidial formation in *Cladosporium*, *Alternaria*, etc. On the other hand the conidial formation may be basigenous, i.e. each new conidium is produced at the apex of the conidiophore just below the last formed conidium (e.g. Erysiphaceae, Aspergillaceae). A third method of formation of chains of conidia is the almost simultaneous rounding up of the cells of a simple or branched hypha into catenulate conidia. These conidia then fall apart almost simultaneously (e.g. *Sclerotinia cinerea*, *Oospora*, etc.). Where the conidia formed in this manner are small they are often called "oidia."

The conidiophores may be scattered or crowded or enclosed in a hollow structure provided with an apical opening (i.e. produced in a pycnidium). If the conidiophores become laterally crowded and adherent into a column we have a coremium, such as is formed in species of *Penicillium* under certain environmental conditions.

The conidia themselves may vary greatly in size and shape as well as color and number and arrangement of cells. In general we may distinguish conidia destined for distribution by air currents and those that are distributed by other means. The latter are usually surrounded by a sticky substance when wet and cling to anything with which they come in contact, drying down and becoming firmly attached when dry. When wet by rain such conidia may be scattered by the currents of water running on the surface of the substratum or may be splashed about by the falling rain drops and

carried by the wind which blows these droplets about. Insects may become contaminated with the sticky spores and thus carry the fungus from place to place.

Chlamydospores are very frequent in many of the orders of the Carpomycetaceae. They arise by the rounding up of mycelial cells, filled with food substances, and the production of a thick wall. They may be intercalary or terminal, single or two to many in a series. In some fungi they germinate promptly, in others they are able to remain dormant a long time.

The mycelium usually consists of long, slender, branching hyphae with terminal growth. Usually the cell is several to many times as long as wide. The septa are centrally perforated by a pore which may be small or may approach in size the perforations found in the septa of the Florideae. These pores are often closed by a plug of protein composition, possibly protoplasmic in nature. In the Order Laboulbeniales the cells are short and broad and the whole structure does not resemble typical mycelium. In many species in the Class Basidiomycetaceae peculiar structures called "clamp connections" occur at each septum. These will be described in connection with that class. The mycelium may be packed together laterally into compact strands with a firm hard outer layer, forming long "rhizomorphs" which may extend many meters. In many forms storage organs, sclerotia, are formed in which the hyphae are packed tightly together and the short cells are pressed mutually to become polyhedral in shape. The adjacent cells adhere to form a parenchyma-like tissue, more properly called pseudoparenchyma. The interior cells are filled with stored food and the outer cells are thick walled, almost sclerenchymatous, and usually dark in color. Pseudoparenchyma may also be found in the fruiting bodies of some of the Higher Fungi, such as the perithecia and the apothecia of some of the Ascomycetaceae. True parenchyma is apparently present in some fungi of this group. In parasitic species the mycelium often sends haustoria of various shapes into the host cells.

Unlike the Lower Fungi whose fruiting structures are microscopic or at most only a few millimeters or centimeters in length (some Mucorales) the fruiting bodies of the Higher Fungi often attain considerable size. Thus *Calvatia maxima*, the Giant Puffball, has been recorded by C. E. Bessey as producing a spore-fruit 1.6

meters long, 1.35 meters wide and about 24 centimeters high. That of *Fomes laricis* sometimes (rarely it is true) reaches a height of 60 centimeters and a diameter of 15 to 20 centimeters. Specimens of a form of *Agaricus arvensis* collected by the author had a pileus diameter of 30 centimeters, and the author has collected a specimen of a species of *Peziza* with an apothecium 40 centimeters in its greatest diameter. Such enormous spore-fruits produce almost incredible numbers of spores. Thus Buller estimated that a puff-ball $40 \times 28 \times 20$ cm. would produce about seven trillion (7,000,000,000,000) spores. At the same rate the enormous puff-ball mentioned above would produce about one hundred sixty trillion (160,000,000,000,000) spores. A spore-fruit of *Fomes applanatus* with an area of one square foot lower surface, produced 30,000,000,000 spores a day for about six months, or a total of over 5,000,000,000,000 spores. A specimen of *Agaricus campestris* only 8 cm. in diameter produced over 1,800,000,000 spores at the rate of about 40,000,000 spores per hour. At this rate the *Agaricus arvensis* found by the author would have produced about 27,000,000,000 spores. On the other hand many of the Higher Fungi have microscopic spore fruits.

In the majority of species the vegetative mycelium is colorless and that is true of the reproductive structures in many cases. In rhizomorphs and the outer layer of cells of sclerotia and sometimes individual hyphae the color may be dark. This color seems to reside in the cell wall and is probably related chemically to melanin. Some fungi produce pigments in the interior of the hyphae. These may be soluble in various solvents and are sometimes variable in color depending upon the chemical reaction. Thus *Fusarium sesami*, studied by the author, produces a red or violet-colored pigment that turns blue when the surrounding medium becomes alkaline. It is soluble in acids and the red form is soluble in neutral salts of various acids. Litmus is the product of the cells of one of the lichen-producing fungi as is orcein. Some hyphae cause a coloration of the substratum in which they are growing. Thus wood in which *Chlorosplenium aeruginosum* is growing takes on a green color, due to a pigment secreted by the mycelium. The reproductive structures are in the majority of cases colored, the pigments being in some cases within the cell (e.g. the bright red color of the hymenium of some *Pezizales*), in other cases in the cell wall. The latter

is mostly the case with the light to dark brown or almost black coloration found in the majority of apothecia and perithecia and in the teliospores of Rusts and Smuts, the spore fruits of Tremellales, Auriculariales, etc. The fungus pigments, especially those occurring in the lichen-producing fungi, have been studied by various authors (Zopf, Milburn and others) but no really comprehensive modern study has been made of the subject taking advantage of the more recent investigations in Organic Chemistry.

The Higher Fungi were called by Charles E. Bessey the Phylum *Carpomycetaceae*, i.e. fruit-producing fungi, in reference to the production of spore-fruits in this phylum. The name *Eumycetaceae* is often applied to this group but is here discarded in view of the fact that this name has also been applied to all the filamentous fungi in contrast with the non-filamentous *Mycetozoa*, *Chytridiales*, etc. They are divided into several classes whose distinctions are based on the type of the ultimate reproductive cells of the spore fruits, as follows:

CLASS ASCOMYCETAEAE.—The ultimate reproductive cells of the spore fruit are ascospores, produced, usually eight in number, within a cell called an ascus, which starts out as a dicaryon cell in which the nuclei fuse, then divide meiotically until the eight nuclei are produced around which the ascospores arise. Over 37,000 species described up to 1925.

CLASS TELIOSPOREAE.—The ultimate reproductive cells of the spore fruit are the sporidia, borne externally, mostly in fours, on the promycelium, an outgrowth from the teliospore. The latter is primitively binucleate, the nuclei fusing as the teliospore approaches maturity. This class is, by perhaps the majority of mycologists, more often included in the following class. Its limits coincide rather closely with the *Hypodermii* which form Order IV of Class IV, *Coniomycetes*, of Elias Fries. About 6500 species recognized up to 1925.

CLASS BASIDIOMYCETAEAE.—The ultimate reproductive cells of the spore fruit are the basidiospores, borne externally, mostly by fours, on the outside of a cell called the basidium which was originally a dicaryon cell in which the two nuclei united. About 18,000 species described up to 1925.

Ascus, teliospore and basidium appear to be homologous structures, originating as binucleate cells in which karyogamy occurs, followed by reduction divisions of the fusion nucleus, the nuclei

thus formed becoming the nuclei of the ascospores, sporidia or basidiospores, respectively.

In addition to these three (or two) classes there is another class, the **FUNGI IMPERFECTI**, often called Deuteromyceteae, consisting of fungi whose vegetative structures or mode of asexual reproduction show their relationship to the Higher Fungi, but which lack any sexual type of reproduction or structures substituted for such sexual reproduction. Perhaps the majority are asexual stages of Ascomyceteae though some are undoubtedly asexual stages of Basidiomyceteae. Until the perfect (sexual) stages can be found their true relationship can not be ascertained. About 25,000 species recognized up to 1925.

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CHAPTER VII

CLASS ASCOMYCETEA: LABOULBENIALES AND DISCOMYCETES

The members at the two extremes of this class have little in common beyond the production of the ascus. The type of sexual union (which is often absent), the plan of the spore-fruit, even the nature and the size of the vegetative mycelium vary tremendously. At the one extreme we find the Yeasts (Order Saccharomycetales) in some of which the unicellular plant becomes transformed directly into an ascus, while near the other extreme are the "Discomycetes" (Order Lecanorales, Order Pezizales, etc.) in which there is a well developed mycelium and in some species a sexual union of a non-motile sperm with a trichogyne, leading to the production of a well organized apothecium with many asci.

It is therefore essential to study the ascus, as being the one structure common to all Ascomyceteae. Omitting the apogamous forms for the present, we find the young ascus to be a binucleate cell (Figure 44, *E*) well supplied with food. The two nuclei are usually considerably larger than those of the vegetative mycelium. The nuclei fuse (Figure 44, *F*), forming a nucleus with double the number of chromosomes found in each of the original pair. This nucleus usually enlarges quite considerably. It divides by meiotic divisions to form four nuclei which in the great majority of cases divide again. In a few species the nuclear division may be repeated until 16, 32, 64 or more nuclei are present in the young ascus. In one species of *Pleurage* the number, according to L. M. Ames,* is 512 while in *Thelebolus stercoreus* the number is over one thousand. Around each nucleus a part of the ascus cytoplasm gathers and is soon set off from the remaining ascus cytoplasm (epiplasm) by a cell wall (Figure 44, *D*). The epiplasm may assist in the formation of the outside layer of the ascospore wall (episporium) which is often beautifully sculptured. The cytoplasm of the ascospore builds

* In a letter to the author.

the endospore, the inner layer of the spore wall. The spore nucleus may subsequently divide followed by septum formation so that the ascospore may eventually be two-celled or even multicellular, though perhaps the one-celled condition is the more frequent, as it is probably the more primitive.

The ascus varies in shape from cylindrical or clavate (Figure 44, *D*), in those forms with a well-developed hymenium, to ovoid or subglobose in those in which the asci are scattered or only loosely clustered. The ascospores escape in various manners. In many cases, particularly in the forms with a typical hymenium, the asci absorb water as they reach maturity and become considerably distended. At the apex there is an area which undergoes softening and stretching until the wall suddenly gives way under the pressure from within the ascus (Figure 50, *C*), permitting the escape of the epiplasm, ascospores and vacuolar liquid while the ascus wall contracts. The ascospores may be shot off for a distance of several centimeters, many times the length of the ascus. In some families of Ascomyceteae the apex of the ascus develops a little lid (operculum) which is forced out, often remaining attached by one edge like a trap door (Figure 50, *A*). In many Ascomyceteae the whole ascus undergoes digestion at maturity, thus setting free the ascospores in a mucilaginous liquid. Other methods of ascus dehiscence or rupture have been reported by Atanasoff, Falck, Ziegenspeck and other investigators.

The spore-fruits of the Ascomyceteae may be classified in general as either apothecia or perithecia or as stromatic structures not referable to either of these forms. In addition there are structures which fit none of these categories such as the naked asci of the Order Saccharomycetales and possibly the spore-fruits of the Order Laboulbeniales.

In the typical apothecium (Figure 46, *B*; 51, 52) we find a disk or saucer-shaped or even cup-like structure usually from a few millimeters up to several centimeters in diameter. The texture is usually fleshy, fragile to tough, sometimes leathery, and the color from pale brown to black, sometimes red, yellow or other colors. The upper surface constitutes the hymenium, a layer of elongated cells standing at right angles to the surface like a palisade. It consists of asci intermingled with supporting and protective cells or hyphae, the paraphyses. Immediately below the hymenium is a

layer, thin or fairly thick, the hypothecium, consisting mainly of light-colored hyphae running parallel to the surface of the hymenium. Often sharply contrasted with the hypothecium, sometimes grading into it is the excipulum which makes up the larger part of the basal portion of the apothecium. Its tissue may be pseudoparenchymatous or may be formed of interwoven hyphae. The outer (lower) surface may be filamentous or may resemble an epidermis. Varying from this type we may find apothecia borne on stipes (as in *Sclerotinia* Figure 55, *A*) or the hymenium may be convex (as in *Pyronema*). In some cases the body of the apothecium is bent back along the stipe so as to form a clavate structure with the upper part covered by an external hymenium (e.g. *Geoglossum* Figure 58, *A*, *Morchella* Figure 54). In other cases the apothecium is subterranean and variously folded internally to form passages and chambers lined by the hymenium (various Tuberales Figure 60). The apothecium proper is the product of the growth of the hyphae immediately supporting the ascogone, when this organ is present. It may develop upon, underneath or within a more or less fleshy stroma or the stroma may be entirely absent (most Pezizaceae). Corner has made a detailed study of the mode of growth and development of various types of apothecia and concludes that their structure indicates relationship to algal ancestors, possibly a group ancestral to the present Florideae.

The typical perithecium Figure 63, *D* is small, usually less than a millimeter in diameter and more or less spherical in shape. It is more often dark colored and more or less hard and brittle, though not always so. Thus in the forms customarily included in the Order Hypocreales the perithecium may be bright colored and fleshy or leathery. Usually, but not always, there is an apical opening, the ostiole, through which the ascospores eventually escape. It may be a simple opening or may have a low lip or be drawn out to a long slender neck (Figure 66, *A*). As limited by Nannfeldt the true perithecium is lined over the whole inner surface or only in its basal portion by a hymenium composed of thin-walled asci (sometimes thickened at the apex) intermingled with true paraphyses and with periphyses in the ostiolar region. Julian Miller has shown that the true wall of the perithecium lies within a stromatic structure which may simply form a thin, darker colored external layer or may form a massive structure within which numerous perithecia

are embedded (Figure 66, *B, C, E*) or on which the perithecia are seated, each with a thin outer stromatic layer. The true perithecial wall is colorless or light colored and is formed from one or more layers of hyphae arising from the supporting cell of the oogone or antherid, producing a hollow structure surrounding the ascogonium and the ascogenous hyphae and asci which arise from it.

In the works of the older mycologists other structures were also called perithecia, which they often resemble very greatly. The studies of von Höhnelt, Theissen, Nannfeldt and others have shown that these structures are entirely stromatic, without any true perithecial walls, and with single asci or tufts of asci without paraphyses, arising in cavities of the stroma. Fungi with this type of spore fruit form the group *Ascoloculares* of Nannfeldt in contrast to the *Ascohymeniales* which produce apothecia or perithecia in the sense indicated above. A third type of ascocarp with perithecium-like structures, usually without any ostiole, and with the asci scattered throughout the interior, neither in tufts nor forming a hymenium, is considered by some mycologists to be a true perithecium, by others to be of a different nature. Fungi with this type of spore fruit form the *Plectascales* of Nannfeldt and others.

An appreciation of the characteristic sexual reproductive processes in the more complex Ascomycetae can perhaps best be obtained by a study of the phenomena in *Pyronema confluens* (Figure 44). This is by no means a very primitive form nor is it a simple structure. It illustrates, however, most of the features that occur in this class. This fungus is found in Nature most frequently on patches of soil where there has been a fire recently, such as the site of a campfire. It also appears frequently in greenhouses on flower pots that have been steamed to sterilize the soil. At first there appears a thin whitish moldy growth on which arise groups of orange-colored apothecia which soon give the whole surface of the soil an orange color lasting only a few days, after which the fungus disappears, to be followed by other fungi. The mycelium is colorless and septate, with its cells mostly multinucleate. Tufted branches are produced, each bearing terminally a more or less spherical, multinucleate oogone, from whose apex there grows out a curved hypha, also multinucleate, the trichogyne. From one of the basal cells supporting the oogone arises an obovoid or clavate multinucleate antherid. The trichogyne grows to the antherid

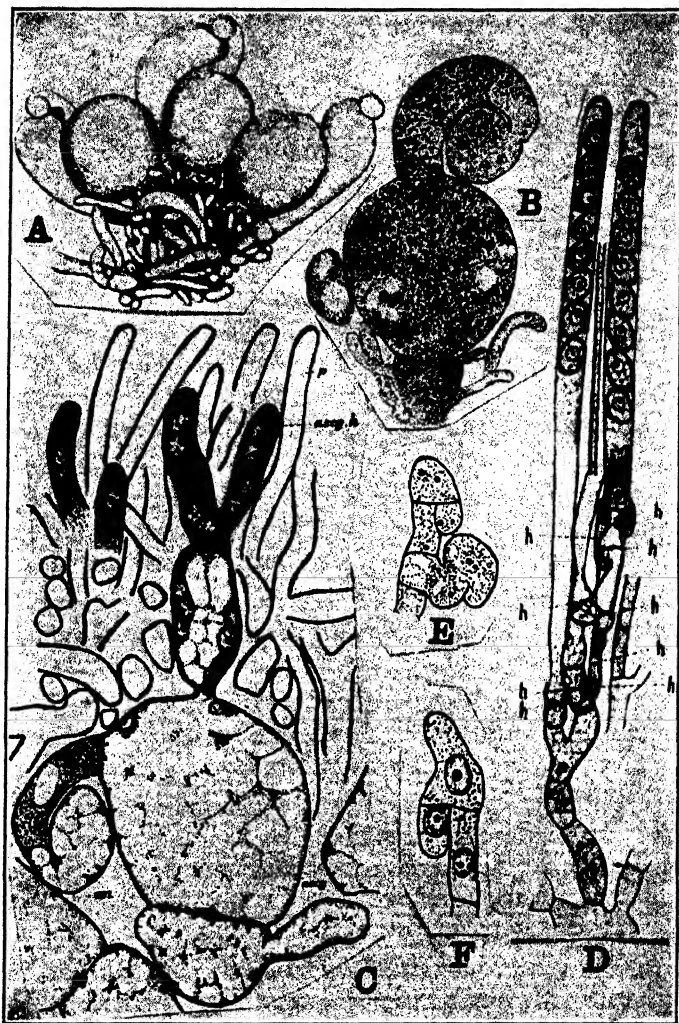


FIG. 44.—Pezizales. *Pyronema confuens*, sexual reproduction. A, group of oogones and antherids; B, section through oogone, trichogyne and apex of antherid, showing opening from the latter into trichogyne; C, similar section, later stage, showing young, forked ascogenous hypha; D, ascogenous hypha from oogone to ascus; E, ascogenous hypha showing two hooks; F, terminal hook of ascogenous hypha with nuclei united in the cell destined to become the ascus. (A, B, E and F after Harper, 1900; C and D after Claussen, 1912.)

and coils upon or around its apex. An opening is then formed from one to the other. The majority of the hundred or more antheridial nuclei pass into the trichogyne, whose nuclei have already begun to degenerate, and then through an opening in the septum at the base of the trichogyne into the oogone which itself contains 100 to 200 nuclei. Here they pair with the oogone nuclei. According to Harper and to Gwynne-Vaughan and Williamson the paired nuclei fuse, forming about half as many diploid zygote nuclei. According to Claussen they do not fuse but merely pair closely. According to Dangeard and his followers no opening is formed between the trichogyne and the antherid (which he considers as a degenerate structure and calls the trophogone), and the nuclei in the antherid and trichogyne disintegrate *in situ*, the oogone nuclei then arranging themselves in pairs. Following this stage all agree that soon 10 to 20 buds appear on the surface of the oogone and elongate to ascogenous hyphae into which the diploid zygote nuclei (or the pairs of haploid nuclei) pass until many nuclei are present in each hypha. The nuclei probably divide in the oogone as some of them do in the ascogenous hyphae. The latter elongate, forking somewhat. Eventually septa are formed, forming cells that are plurinucleate toward the base of each ascogenous hypha and fewer nucleate toward the apex where the last few cells are binucleate. In the meantime from the cells supporting the tufts of oogones and antherids there have been growing outward and upward numerous hyphae which intermingle with the ascogenous hyphae derived from the oogone and also form a mass of hyphae externally. From the terminal binucleate cell of each ascogenous hypha a lateral branch forms just beneath the apex and the two nuclei divide simultaneously (conjugate division) so that the lateral cell also becomes a dicaryon (binucleate) cell. This may be repeated. Eventually the numerous terminal dicaryon cells so produced proceed to the production of the asci. The cell curves back upon itself like a hook with the pair of nuclei in the curve. The nuclei divide conjugately and cross walls are formed, leaving two of the nuclei (a daughter nucleus of each of the two original nuclei) at the curve and one daughter nucleus in the cell at the tip of the hook and another daughter nucleus in the cell cut off at the base of the hook. The two nuclei in the curve of the hook fuse while the cell elongates. This is the young ascus. The basal and apical cells

of the hook may fuse and then elongate and form a new hook and a new ascus, etc. The fusion nucleus of the young ascus is diploid or tetraploid according to the interpretation as to the presence or absence of nuclear fusion in the oogone. This nucleus by three successive divisions produces eight nuclei. The first two divisions are reduction divisions (meiosis) according to either theory, the third division being considered the final division of a second meiosis by the advocates of the tetraploid nature of the young ascus nucleus. By both theories the eight resulting nuclei are haploid. From the centrosome remaining in close proximity to each of the eight nuclei fibrillae appear to radiate and certain of these rays curve downward around the nucleus, at some little distance from it, apparently delimiting a mass of cytoplasm surrounding the nucleus from the remainder of the cytoplasm of the ascus, the epiplasm. Along this delimiting surface the ascospore wall is laid down. In the meantime the asci have been elongating as have the vegetative hyphae surrounding and between them. The latter become the paraphyses while the former form the marginal tissues of the apothecium. The body of the apothecium consists then of the several oogones and the branched ascogenous hyphae which grew out of these, of the antherids, and of the vegetative hyphae which arose from the supporting cells of the oogones and antherids. These latter form the main body of the apothecium as well as its paraphyses. In the excipulum these hyphal cells by lateral enlargement and mutual pressure form a pseudoparenchymatous tissue.

It may seem strange that so common a species, the subject of numerous investigations by different investigators should still be the subject of so much disagreement. Perhaps the difficulty of staining well the rather small nuclei and the rapidity of the progress of the sexual phenomena are responsible for the greater part of the difficulty encountered. To this must be added the fact that many of the stages of development, if the exact sequence is not certain, could be interpreted differently if considered as belonging to an earlier or later stage. Furthermore, an investigator, with the best will possible, is apt to interpret what he sees in the light of what appears to him to be the most logical series of events.

Using the phenomena just described for *Pyronema* as a basis for comparisons we find that sexual reproduction has many different forms in the Ascomyceteae. Thus the antherid when present may

not be a functional organ. This is clearly the case in *Pyronema confluens* var. *inigneum* in which W. H. Brown has shown that there is no opening between antherid and trichogyne and frequently no contact. Dangeard denies the functioning of the antherid in the whole class except in the Order Saccharomycetales. He accounts for the pairs of nuclei in the oogone and ascogenous hyphae as a pairing of the female nuclei, which seems to be beyond doubt the case in the variety of *Pyronema* just mentioned. For Dangeard the only nuclear fusion is that occurring in the ascus. For those following Claussen this is the true nuclear fusion (karyogamy) but the union of antherid and oogone is looked upon as a true sexual fusion also (cytogamy). Harper and Gwynne-Vaughan and Williamson believe cytogamy and karyogamy to occur one just after the other, with a second nuclear fusion occurring in the ascus.

There is a marked tendency to the production of a more or less coiled series of cells, usually considerably greater in diameter than the cells of the vegetative mycelium and often tapering to a long, slender, multicellular trichogyne. Such a structure is called an ascogonium and the cell out of which the ascogenous hyphae bud may properly be considered the true oogone. This may be multinucleate or uninucleate. In the Laboulbeniales, a few genera of the Lecanorales and apparently also in a few of the Pezizales and Sphaeriales minute non-motile sperms are produced on short antheridial branches and upon reaching the trichogyne fuse with it, the sperm nucleus entering and passing from cell to cell to the oogone. In other cases the trichogyne fuses with an antherid without the formation of separate sperm cells. We find all degrees of reduction from the multicellular ascogonium with a long trichogyne to the one-celled oogone with one-celled trichogyne as it occurs in *Pyronema*. In many cases the trichogyne is lacking, so that the antherid comes into direct connection with the oogone. Sometimes no antherid at all is formed. In such a case fusion of nuclei often does not occur in the oogone but the female nucleus divides and paired haploid nuclei pass out into the ascogenous hyphae. In *Humaria granulata*, which does not possess an antherid, Gwynne-Vaughan and Williamson report that the oogone nuclei unite by pairs and these zygote nuclei pass out into the ascogenous hyphae. Apparently a cell of the series of ascogonial cells may in some cases be substituted in function for an antherid, its nucleus taking the

place of the antherid nucleus. Sometimes no recognizable oogone or ascogonial cells can be found. Some of the vegetative hyphae of the spore fruit become converted, in a manner not known, into ascogenous hyphae with dicaryon cells. In many families of Ascomyceteae the terminal cell or cells or the ascogenous hypha become asci without the formation of the hook described for *Pyronema*. The two nuclei of the cell fuse and the cell enlarges terminally or laterally, with successive nuclear divisions and ascospore development. In the sexual species of the Order Saccharomycetales two cells fuse to form a single ascus and no ascogenous hyphae are produced. Kharbush reports a similar origin of the asci in the highly developed apothecium of *Sclerotinia fuckeliana*. In this apothecium, according to him, there are no distinguishable ascogenous hyphae. At the base of the hymenium the apices of adjacent hyphae unite and the nuclei fuse, thus giving rise to the young asci, one fusion of paired hyphae for each ascus.* The opposite extreme is *Taphrina* (*Exoascus*) in which Wieben has shown that the ascospores are of two opposite sexual tendencies, four of each tendency within the ascus. These ascospores or the spores that bud off from them give rise to slender germ tubes which fuse with those from ascospores of opposite sexual tendency, giving rise to a dicaryon mycelium which is the vegetative mycelium that infects the host. Eventually some of the cells of this mycelium enlarge, the nuclei fuse and the asci are formed. Thus in *Sclerotinia fuckeliana*, if Kharbush's report is correct, the mycelium and the apothecium lack entirely the dicaryon phase except as the cells fuse to initiate the asci, while in *Taphrina* the whole vegetative mycelium is of dicaryon nature.

Some botanists (B. O. Dodge, E. A. Bessey) suggest that the production of non-motile sperms which fuse with trichogynes and the budding out of ascogenous hyphae from the oogone are indications that the Ascomyceteae may have descended from some algae related to the Red Seaweeds (Florideae). Other botanists (e.g. Gäumann, Atkinson, Nannfeldt) consider the non-motile cells that fuse with the trichogyne merely to be modified conidia which have been substituted for antherids, just as certain fusions of vegetative cells have taken the place of the union of sexual organs in the Class

* In view of the entirely different mode of sexual reproduction reported by Drayton for *Sclerotinia gladioli* it is evident that the process in *S. fuckeliana* needs reexamination.

Basidiomycetae. Dangeard and the Moreaus deny any fusion of sperms and trichogyne, at least so far as any transference of nuclei occurs. Since the author follows those that consider the production of a trichogyne and non-motile sperms, and of an oogone from which branch out numerous ascogenous hyphae to be primitive characters for the class the orders will be arranged in a sequence from that viewpoint. Those botanists who see nothing more than an accidental convergence of structures in the occurrence of these organs in both Ascomycetae and Florideae would preferably start with the Order Saccharomycetales and work back to the Lecanorales and Laboulbeniales which would be considered by them the orders the furthest removed from the primitive Ascomycetae.

Order Laboulbeniales.—These are minute, almost microscopic parasites upon insects. They develop externally upon the host except for a haustorium or "foot" that is rooted in the chitinous body wall of the host or less often may penetrate it and form a branching hyphal growth in the body cavity. In the commoner method the foot usually enters the body wall at a pore and thus obtains an ample supply of food without penetrating clear into the body cavity. The fungi vary from plants only a few cells in number (Figure 45, *A, F*) and considerably less than 0.1 mm. in height to forms with hundreds of cells and 2 or 3 or more millimeters tall. The cell walls are usually thick and firm, often dark in color. The plant may consist essentially of a row of cells which gives off laterally some branched filamentous appendages and a female reproductive branch. On or near the appendages are borne the antherids. This simple type of structure may become more complex by the longitudinal division of the cells to form a body several cells in thickness from whose sides the appendages and the male and female sexual organs may arise. In *Zodiomyces vorticellarius* (Figure 45, *G*) the main plant body is multicellular and wider at the top, bearing on the flattened upper surface many filamentous appendages and the sexual organs. Some of the larger forms lie prostrate on the body of the host, rooting at various points by means of rhizoids. Between adjacent cells which have arisen by the division of a common parent cell there is distinctly visible a perforation in the septum as is usual in the Class Florideae.

In most of the genera of the order the antherids are flask-shaped organs (Figure 45, *E*). The apex opens and a uninucleate sperm

is pushed up into the neck by the division of the nucleus and cytoplasm of the body of the antherid. By successive formation of sperms in this way those previously formed are pushed out of the

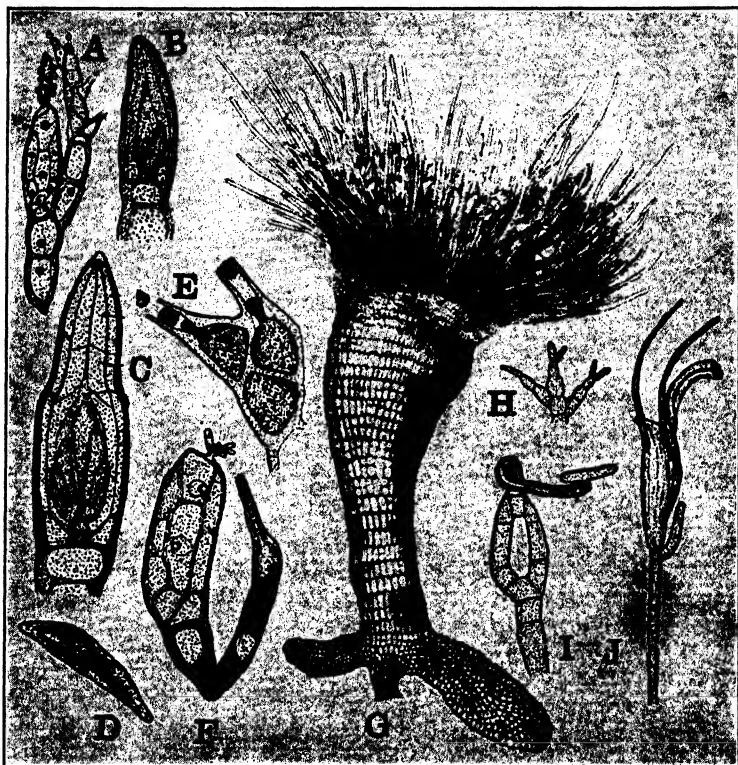


FIG. 45.—Laboulbeniales. A-E, *Stigmatomyces baeri*. A, mature plant showing at the right the appendage with several antherids and at the left the enclosed oogone and the papillate trichogyne; B, the fertilized oogone has divided into two basal cells and several upper cells; C, asci are budding out of some of these upper cells of the oogone; D, an ascus; E, two antherids with escaping sperms; F, *Amorphomyces fulagriae*, adjacent male and female plants; G-J, *Zodiomyces vorticellarius*; G, Mature plant; H, antheridial branch, note exogenous sperms; I, oogonial branch with trichogyne bearing attached sperm; J, mature ascocarp. (All after Thaxter, 1895.)

neck. These sperms are apparently naked cells, entirely devoid of cilia or flagella. Sometimes several flask-shaped antherids open into a common cavity with a single opening to the outside. In a few genera the sperms are produced by the abstriction of a terminal

cell of a short slender branch from an appendage (Figure 45, *H*). Such sperms appear to possess a very thin cell wall.

The female reproductive branch ("archicarp" of some authors) usually consists of a row of three cells (Figure 45, *A, F*), from the base to the apex respectively the oogone ("carpogenic cell"), trichophore and trichogyne. The first two are nearly or completely surrounded by, usually, a single layer of closely adhering protective cells. The trichogyne is usually one-celled but may divide into several cells and is simple or extensively branched. Perhaps in most cases the sperms are brought into contact with the trichogyne by the active movements of the insect host as it brushes against surrounding objects or other insects. Possibly in the case of aquatic insects or those frequenting wet places water currents may bring about the transfer of sperms to trichogyne. In the genus *Zodiomyces* the elongated trichogyne seeks out and unites with the sperm (Figure 45, *I*). In some species antherids are unknown and the further development of the oogone is probably apogamous.

After fertilization the oogone divides into about three cells, the binucleate middle cell of which now buds out laterally (Figure 45, *B, C*) on all sides to form numerous binucleate asci in which the two nuclei fuse and then divide in the usual way to form eight nuclei. All eight or only four of these nuclei serve as the centers of origin of the ascospores, in the latter case the other four nuclei undergoing degeneration. The ascospores usually are elongated and become two celled. The ascus walls digest and leave the numerous ascospores in a probably somewhat sticky gum in the cavity of the considerably enlarged spore-fruit whose walls have increased in thickness. Eventually the ascospores are discharged between the apical cells and because of their sticky walls adhere to objects with which they come into contact, such as the body of another insect. In the latter case they germinate, one cell becoming the foot and the other developing the remainder of the plant. The full nuclear phenomena of fertilization have not been worked out because of the difficulty of finding the fungi in the proper stages of development and the extremely difficult technique of sectioning and staining.

Only a very few genera and but few species of this order were known until the monumental work of the recently deceased Dr. Roland Thaxter, published in successive parts in 1896, 1908, 1924, 1926 and 1931, revealed the fact that this order contains hundreds

of species, dozens of genera and several families. Since the appearance of the first volume of this marvellous work other mycologists have also added numerous species to those described by Dr. Thaxter. Not only are these fungi found on beetles (Coleoptera) but also on Hymenoptera, Diptera and various other orders of insects. In view of the fact that of the 1,500,000 described species (and possibly 4,000,000 or so as yet undescribed species) of insects only a few thousand have been examined for the presence of these parasites it seems reasonable to suppose that the number of species, genera and even families of this order may be greatly increased in the future.

The relationship of the Laboulbeniales to other Ascomyceteae is very distant. The spore-fruit is unlike that of any other members of this class and the vegetative structure finds few analogies. In the sexual reproduction the production of functional, separable sperm cells is known in *Collema* among the lichens and in Pezizales, Sphaeriales and possibly other groups. In most of these, however, the sperms are not produced endogenously as naked sperms as is true of most of the Laboulbeniales. The "archicarp" reminds one remarkably of the condition in some of the Florideae where the archicarp is surrounded by protective cell layers with merely the trichogyne exposed. The budding off of the asci from the fertilized oogone is comparable to the budding of the short carposporic branches from the fertilized oogone of the Red Seaweeds. These latter organisms also produce non-motile, naked sperms, often pushed out of the antherid by the subsequently formed sperms. The pores between adjacent cells are also conspicuous in the Red Seaweeds. Hence it is possible to imagine that some fresh-water Red Seaweeds that had adopted a habitat on the bodies of aquatic animals acquired the parasitic habit (as known among some species growing upon other Red Seaweeds) and by the transformation of the carpospores into asci gave rise to the ancestors of this group of organisms. It must be admitted that the substitution of an ascus for a carpospore requires a series of modifications of which we know no traces of intermediate steps unless the ascus is considered as a modification of a tetrasporangium. Furthermore, it must be noted that the Red Seaweeds possess cell walls of the nature of pectose and cellulose while chitin (in addition to carbohydrates) is present in the cell walls of most Ascomyceteae.

The following orders; Lecanorales, Pezizales, Tuberales, Hysteriales and Taphrinales all produce spore-fruits that may be considered as typical or modified apothecia. They are often all or in part included in the group name Discomycetes.

Order Lecanorales.—The Disk Lichens.—These constitute a large group of organisms which have in common the production of apothecia and which show a specialized form of parasitism on land species of Chlorophyceae and Myxophyceae. The validity of the maintenance of this group apart from the Pezizales is, to say the least, very doubtful, but until the reproductive processes, especially the behavior of the sexual nuclei, are better known in both groups it is perhaps better to follow custom and consider the two orders separately. Possibly when such studies have been carried out in all the more important genera that produce apothecia the system of classification of both orders will have to be entirely revised.

Vegetatively the Lecanorales vary from a loose branching mycelium penetrating in all directions the gummy colony of a species of *Nostoc*, the form of that colony setting the limits to the size and shape of the lichen body (*Collema*), to a very complexly branched, firm thallus with an epidermis-like outer layer of hyphae enclosing the algal hosts and thus making possible unlimited growth, without reference to the natural shape of the unparasitized algal colony (Figure 46).

The mycelium is in general slender, light colored, septate and branching. The septa are centrally pierced by a rather minute perforation. In the forms with a cortex (the majority of lichens) the mycelial cells composing it are short, broad, rather thick-walled and compacted together into a pseudoparenchyma one to several cells in thickness. In the interior of the lichen the mycelium is filamentous and loose. Usually the algal hosts are found in definite layers. In some cases definite penetration of the algal cell by the mycelium can be observed. Such cells are eventually killed. Geitler reports that more often no such penetration can be seen but the mycelium is applied to the algal cell in the manner of an appressorium. Just how the fungus draws its nourishment from the alga in the absence of direct penetration is a matter of conjecture. Possibly some substance secreted by the fungus increases the permeability of the plasma-membrane of the algal cells, thus per-

mitting sugars and other soluble foodstuffs to diffuse out from the cell to be picked up by the fungus. The fungus furnishes a certain amount of protection to the alga and probably gives it a more equable habitat, protecting it from the rapid extremes of drying and moisture, sun and shade, heat and cold. In so far as this is true it is to the advantage of the alga. On the contrary, the constant tribute levied in the form of food substances diffusing out from

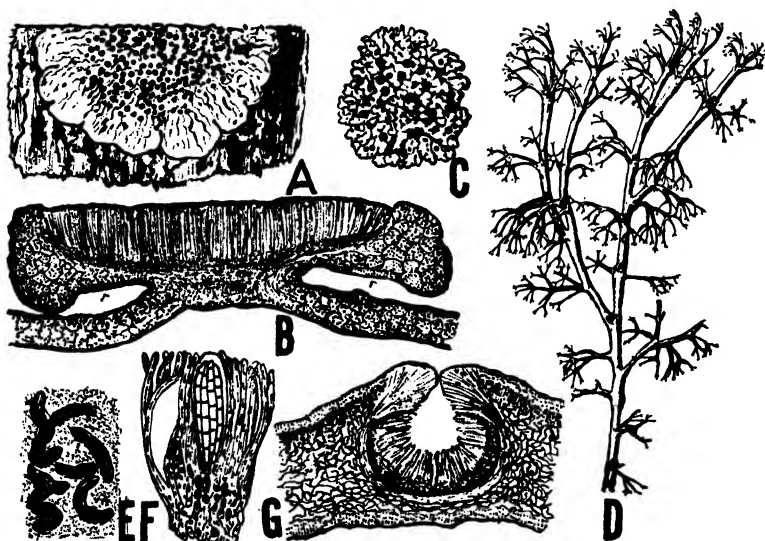


FIG. 46.—Lichens. A, *Collema nigrescens*; B, vertical section through apothecium of *C. cheileum*; C, *Lecanora lentigera*; D, *Cladonia rangiferina*; E, *Graphis elegans*; F, portion of hymenium of *Bacidea rubella*; G, vertical section through perithecium of *Endocarpon minutum*. (A–E and G after Reinke, 1895; F after Galløe, 1929.)

the cells must reduce somewhat their vigor. It is worthy of note that algae whose free-living development includes zoospore formation as a normal mode of reproduction usually have this entirely suppressed, reproduction being limited mainly to fission.

The algal hosts are usually Blue-green Algae (Myxophyceae) or Green Algae (Chlorophyceae) whose habitat consists of moist situations on land, such as on the ground, rocks, trees, etc. More often the one-celled algae are preferred (*Chroococcus*, *Chlorococcum*, etc.), but some of the filamentous forms are also captured and made prisoners (*Nostoc*, *Trentepohlia*, etc.). Most genera of lichens are confined to a single species or to closely related species of algae

but a few lichens are able to use as algal hosts forms from widely diverse groups. It is noteworthy that the thallus formed by the same species of fungus with these widely separated algal hosts is very different, according to the host present.

Lichens may be grouped morphologically in accordance with the type of thallus into crustose, foliose, fruticose and pendent lichens. The first form closely adhering crusts on the substratum to which they are held fast by hyphal strands; the foliose lichens are flat and thin ("leaf-like") but adhere to the substratum only at definite points; the fruticose lichens are upright in habit (Figure 46, *D*) and more or less branched, resembling little shrubs (*frutex* = shrub). The pendent forms are attached only at localized spots and are long, slender and branching, hanging from the twigs or branches of the trees to which they are attached. They are often considered only a special type of fruticose lichen. It must be noted that these distinctions are not absolute for there are gradations between these types. Most species of *Cladonia* are at first foliose (but with small "leaves"), later becoming upright in habit, at which time the prostrate foliar growth may disappear. The distinction between crustose and foliose lichens is not always clear (Compare Figure 46, *A* and *C*).

In tropical and subtropical regions many lichens grow on the algae attached to the surface of leaves. The fungus hyphae may enter through the stomatal openings into the interior of the leaf where it seems probable that they are somewhat parasitic upon the leaf tissues. Rock-inhabiting lichens often penetrate the rock itself some distance by means of their holdfast hyphae. Recently attention has been drawn to serious damage to glass windows in some old churches in France, where the lichens attached themselves to the glass and gradually corroded the latter. Probably the requisite mineral nutrients of the lichen and enclosed algae are obtained by the hyphae that attach the lichen to its substratum. A very few species of lichens develop in aquatic habitats.

In color, lichens vary from gray (greenish-gray when wet because of the color of the enclosed algae) to yellow and other bright colors. Some species are black. The apothecia are frequently brilliant in color on species that otherwise are rather dull colored. Many of the acids extracted from various lichens give rise to brilliant pigments such as orcein, litmus, etc.

But few lichens produce conidia as a means of asexual reproduction. Many lichens have no known asexual mode of reproducing themselves. The pendent forms are frequently torn to pieces by the wind and carried considerable distances, thus achieving distribution. On a great many lichens special asexual reproductive structures are produced, the soredia. In barest details a soredium arises as an outgrowth of the interior mycelium of a thallus, carrying with it some of the algal cells. Having grown out through the surface of the thallus this mycelial mass rounds up into a ball with a sort of cortex, containing in its interior loose hyphae and a few host cells. This structure breaks loose and is distributed by wind or rain to other locations where the hyphae grow fast, thus starting a new lichen thallus.

In their sexual reproduction the Lecanorales are rather uniform in their end product, the apothecium, which differs in its details but not in its fundamental plan in the different families and genera. These variations have to do with shape (concave, flat, convex); color; structure of the paraphyses; number, color, structure and shape of the ascospores (colorless or brown, 1-celled or divided into two or more cells; ellipsoidal, fusoid, needle-like, etc.); structure of the hypothecium; size; location on the thallus; etc. In contrast with the Pezizales the apothecia of the Lecanorales are usually slow in development and persist for a long time, maturing a few asci at intervals. The asci are inoperculate and usually thickened at the apex (Figure 46, *F*). The details of the sexual process, particularly the behavior of the sexual nuclei, are sadly in need of further study in almost all genera of the order. It may be safely said that no lichen has been satisfactorily studied from these stand-points. The conditions in *Collema* and *Collemodus* will illustrate the main features of the sexual process in this order.

In the interior of the lichen *Collema* is formed a slender, branched mycelium, loosely penetrating and limited in outline to the shape of the *Nostoc* colony it inhabits. There is no cortical layer. On this interior mycelium there arise here and there somewhat thicker hyphae which are noticeable because of their dense contents and their more or less loosely coiled structure. These are the ascogonia (Figure 47, *A*). The cells like those of the vegetative mycelium are uninucleate. Each ascogonium consists of from one to three coils of cells terminated by a filament (the trichogyne) which turns

toward and extends just through the surface of the colony. Its exposed tip is slightly larger and covered with a somewhat thickened wall which is sticky when wet. In its multicellular structure it differs greatly from the trichogyne of the Florideae. The male organs are branched hyphae projecting into a conceptacle-like structure (spermagonium Figure 48, *A*) which opens at the surface

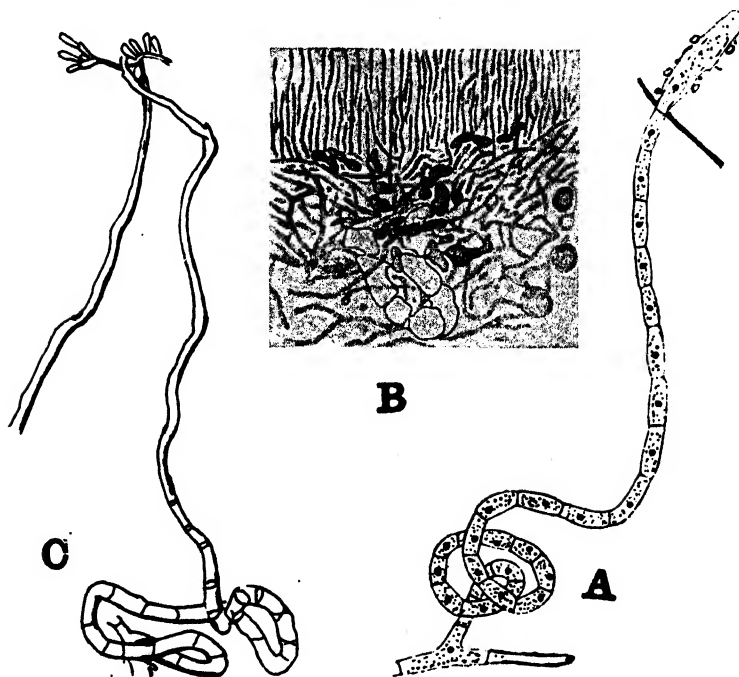


FIG. 47.—Lecanorales. *A*, Ascogonium and trichogyne of *Collema crispum*; *B*, young apothecium of *Anaptychia ciliaris*, showing portion of ascogonial coil and ascogenous hyphae; *C*, *Collemodon bachmannianum*, ascogonium and internal trichogyne reaching a cluster of sperm cells. (*A* after Baur, 1899; *B* after Baur, 1904; *C* after Miss Bachmann, 1912.)

of the colony. From these branches there bud off minute, uninucleate, non-motile sperms (Figure 48, *B*) possessing a delicate cell wall. When wet by rain the gummy mass filling the spermagonium swells and oozes from the opening where the gum dissolves and the sperm cells are carried off by the film of rain water. Such a sperm coming in contact with the sticky tip of the trichogyne adheres to it and Baur has demonstrated that soon an opening is dissolved

through which the sperm nucleus passes into the apical trichogyne cell. Successive swellings and disappearance of the septa of the trichogyne seem to indicate the passage of the sperm nucleus down to the coils of the ascogonium. The nuclear behavior has not been followed in detail, however, owing to the difficulty of finding the right stages and the technical difficulties of staining, etc. From one of the ascogonial cells, which therefore corresponds in function to the oogone of *Pyronema*, ascogenous hyphae begin to grow out-

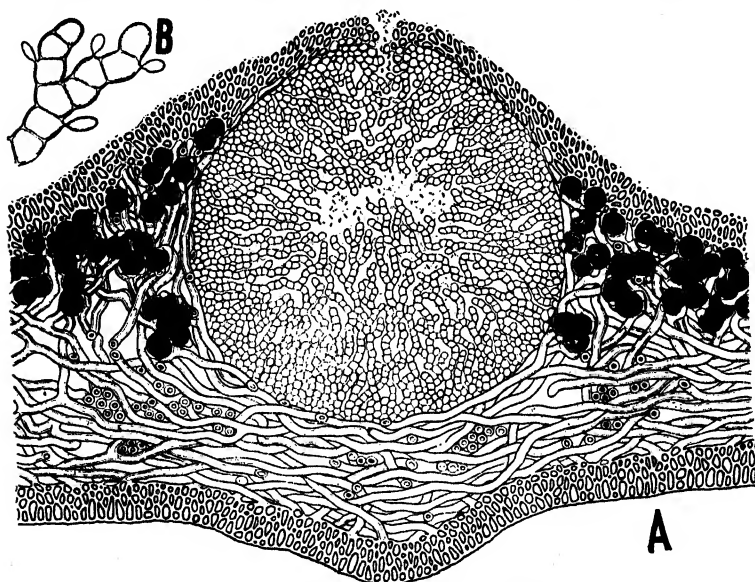


FIG. 48.—Lecanorales. A, Spermagonium of *Physcia* sp.; B, antheridial filament enlarged. (After Kny, Botanische Wandtafeln.)

ward and upward (Figure 47, B). The surrounding vegetative hyphae become actively involved in growth and produce the vegetative part, including the paraphyses, of the apothecium (Figure 46, B) which now develops. The ascogenous hyphae produce their asci by the hook method as described for *Pyronema*.

In the very similar lichen *Collemodon* (erroneously identified with *Collema pulposum* by the investigator) Miss Bachmann found that the branches from which the sperm cells are budded off are not collected in spermagonia but are scattered here and there in the interior of the colony. The ascogonia are similar to those in *Collema* but the trichogynes are longer and do not extend to the surface.

They are attracted chemotropically to the clusters of sperm cells and grow toward them (Figure 47, C), coiling around and uniting with them. The subsequent development is identical with that in *Collema*.

In a number of other genera (e.g. *Physcia*) spermatogonia and trichogynes are produced. Adherence of sperm to trichogyne has been observed but rarely. In a few cases an opening has been observed between sperm and trichogyne but nuclear passage has not been seen. Probably the sperm is functional in most cases of this sort. In those species in which trichogynes have been reported but no spermatogonia are known the condition reported above for *Collema* should be sought for before denying any type of sexual union. In many lichens the ascogonium produces no trichogyne and may even be but a straight row of a few cells. In one or two such cases adjacent cells of the ascogonium lose their intervening septa whereupon ascogenous hyphae begin to appear. Just what the nuclei do in that case can only be surmised. Sexuality seems to be on the decline in this order as throughout the Higher Fungi. The Moreaus have studied the reproduction of many lichens and deny any sexual function to the sperm cells, considering them when present, to be modified conidia.

Because of the possession of a functional trichogyne and the production of separate sperm cells and of asci a certain degree of relationship between the Lecanorales and Laboulbeniales can be postulated, but they are certainly quite widely divergent from their common ancestor. This may have been an alga somewhat like some of the filamentous, freshwater Florideae. It would require the assumption that subsequent to the acquisition of the ascus-producing habit the one series developed as parasites on insects with little modification of the protected procarp while the other series developed as parasites on algae, presumably at first submerged forms, later land algae. At the same time the spore-fruit deviated far from the simpler procarp type shown in the Laboulbeniales. Here again it must be noted that many mycologists hold that the sperm cells are nothing but conidia somewhat modified to take up secondarily the sexual function in place of an antherid. The external similarity between these groups and the Florideae from this viewpoint would be looked upon as a case of convergence, not as an indication of true phylogenetic relationship.

Zahlbruckner believes that the group treated here as a single order, the Lecanorales, is really polyphyletic, i.e. derived from non-lichen forming fungi at many different points. Perhaps the ultimate logical disposition of the lichens will be to distribute them among the other apothecium-forming fungi at the points where their apothecial structure and manner of sexual reproduction seem to fit best. Until the enormous mass of study needed to acquire this information has been carried out it may be best to treat the Disk Lichens as a single order.

The forms here included in the Lecanorales are divided by Zahlbruckner (1926) into about 37 families, about 275 genera and about 7400 species. They occur from the Tropics to the Antarctic and Arctic Zones and from sea level to the tops of the highest mountains where rock is exposed. They furnish the chief food of the caribou, the reindeer and the musk-ox. Some species are used for human food in famine times. Iceland moss, *Cetraria islandica*, is sometimes used for medicine. Litmus and Orcein are derived from lichens. Miss Annie L. Smith's publications on these fungi should be studied for a more complete understanding of this extremely variable group of organisms.

Order Pezizales.—The fungi comprising this order are mostly saprophytes although a number of more or less serious diseases of cultivated plants are caused by parasitic species of this order (e.g. various species of *Sclerotinia*, *Pseudopeziza*, etc.). Those forms that are parasitic do not attack algae in such manner as to produce lichen thalli. Asexual reproduction by means of conidia is found in a good many species but by no means as widely distributed as in some of the orders to be discussed later (e.g. Sphaeriales, Aspergillales). Conidia are formed singly on simple or branched conidiophores or the individual cells of whole segments of mycelium round up to form chains of conidia (*Monilia* type). In a number of species sclerotia are produced in abundance.

In this order we find almost all gradations in sexual reproduction. In *Sclerotinia gladioli* Drayton has shown that minute sperm cells must be brought to certain receptive organs (ascogonia) before apothecia can be produced. In *Ascobolus carbonarius* B. O. Dodge has shown that a much coiled ascogonium bears a long trichogyne which grows to a structure resembling a conidium and attaches itself and fuses with it (Figure 49, A and B). This resembles greatly

what Miss Bachmann described for *Collemodus*. In the genus *Ascobolus* other species have an ascogonium which coils directly around and fuses with an upright antherid (Figure 49, C) while in still other species both Schweizer and Ramlow have shown that antherid and trichogyne are both absent. In *Lachnea stercorea* according to Fraser the oogone is rounded and multinucleate, as in *Pyronema*, but the trichogyne is several celled. S. G. Jones finds in *Pseudopeziza trifolii* the production within the leaf of the host (*Trifolium pratense*) of numerous ascogonial coils which consist of

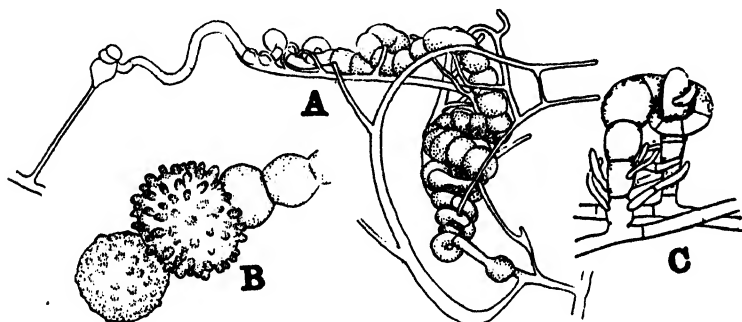


FIG. 49.—Pezizales. A and B, *Ascobolus carbonarius*. A, ascogonium with trichogyne reaching out to a distant antherid (conidium); B, ascogenous hyphae beginning to bud out from ascogonial cells; C, *A. magnificus*, ascogonium and antherid. (A and B, after Dodge, 1912, C after Dodge, 1920.)

heavily staining uninucleate cells. Around these but without any visible cell fusions the vegetative mycelium develops into actively growing hyphae, some of which emerge from the stomata, the so-called "trichogynes," to which Jones denies any reproductive function, considering them to be "respiratory hyphae." Other hyphae become true ascogenous hyphae with binucleate cells, and still others produce the paraphyses and other portions of the apothecium while the original ascogonium degenerates without having served any other function than as a center of attraction for the surrounding hyphae. There is a nuclear fusion in each young ascus and only the first of the following three nuclear divisions is reductional. In some Pezizales even the oogone or ascogonium is not to be found. The eventual product is an apothecium which in its general plan is like that of the Lecanorales but usually larger and more fleshy.

In this order two series of forms may be distinguished, depending upon the mode of dehiscence of the ascus at maturity, viz. the Operculatae and the Inoperculatae (Figure 50, *A* and *C*). In the former, a little lid (operculum) is formed at the apex of each ascus which gives way when the turgor pressure reaches a certain point, thus allowing the escape of the ascospores and surrounding liquid. The operculum may be shot off entirely but more often remains attached at one edge like a trap door. In the Inoperculatae the thickened apex of the ascus gradually softens and yields to the internal pressure, forming a pore through which the ascus contents escape.

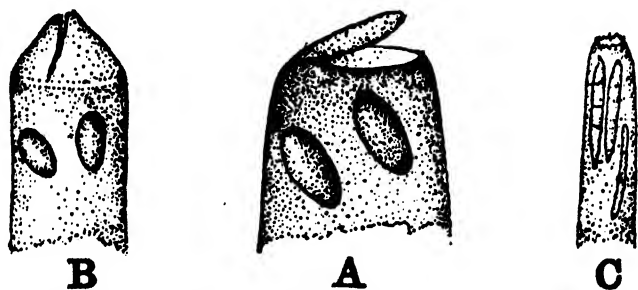


FIG. 50.—Pezizales. Methods of dehiscence of ascus. *A*, operculate; *B*, bilabiate; *C*, inoperculate. (After Seaver, 1928.)

In this order the ascospores are one-celled and ellipsoidal to subspherical to a much greater extent than in the Lecanorales where many-celled ascospores are common.

The apothecia in this order vary greatly in size. In a few species of *Ascobolus* and some other genera the apothecium is less than a millimeter in diameter; in the larger number of genera and species it is from five to ten or twenty millimeters in diameter, while as mentioned before, the author has collected an apothecium of a species of *Peziza* with a length of 40 centimeters and about 30 centimeters wide. The shape is also subject to great variation. In *Pyronema* and some other genera the apothecium is convex and naked from the beginning. In more forms it is flat or cup shaped. In most of them the hymenial surface is at first covered with a more or less evanescent layer. Some species have a subspherical apothecium, at first closed and opening by an enlarging pore or ostiole at the apex. The apothecium is more often sessile but yet is stalked in many genera. A few genera produce their apothecia just under

the surface of the soil, opening by a small pore at the surface when the apothecium is mature. In *Cyttaria*, parasitic on twigs of the Southern Beech (*Nothofagus*), there is formed a fleshy stroma several centimeters in diameter in whose outer half or more the small

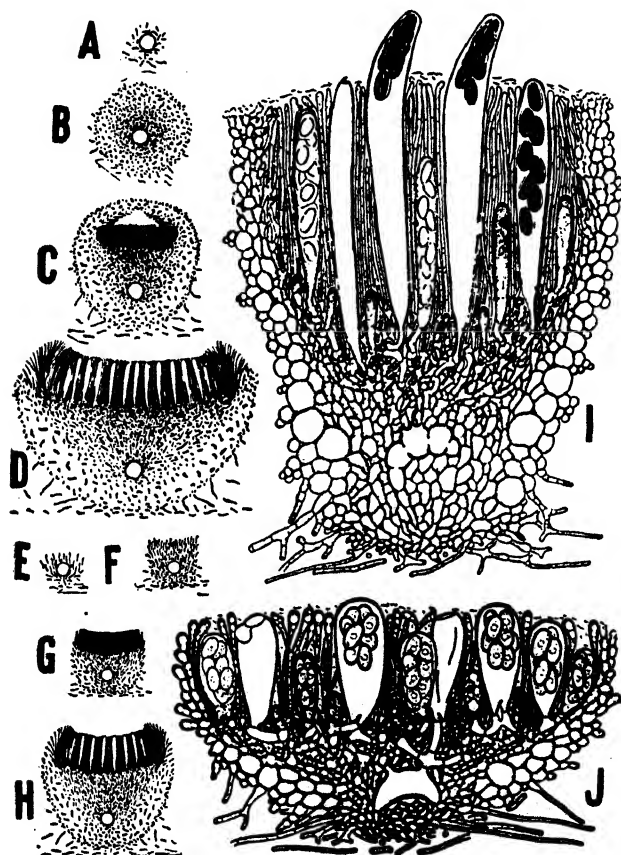


FIG. 51.—Pezizales. A–D, diagram of development of angiocarpic apothecium; E–H, development of gymnocarpic apothecium; I, apothecium of *Ascobolus stercorarius*; J, apothecium of *Ascophanus granuliformis*. (After Corner, 1929.)

apothecia arise (Figure 59). These are at first closed but at maturity open at the surface of the stroma.

A noticeable feature of the larger apothecia of the whole order is the simultaneous discharge of ascospores over a large portion of the hymenium. This discharge has been reported often as being accom-

panied by a hissing sound, as has been verified by the author. The distance to which the spores may be discharged is remarkable, sometimes several centimeters. Falck has shown that the discharge of ascospores is dependent to a considerable degree upon changes in temperature or illumination or upon contact of some other object with the apothecium. Even the stimulus of a gentle current of air is sufficient to cause spore discharge with some species. In species of *Ascobolus* and other genera the ascus at maturity becomes greatly elongated and distended laterally by the absorption of a large amount of water (Figure 51, I). When the operculum gives way the greatly enlarged ascus contracts with great violence and the contained liquid and ascospores are ejected to an amazing distance. In *Saccobolus* the ascospores are massed together in a ball which is expelled further than would be possible for separate spores.

It has been shown that differentiation into two distinct sexual strains occurs among some species of this order. Thus Miss Green has shown for *Ascobolus stercorarius* and Betts for *A. carbonarius* that they will not produce apothecia when grown in culture from a single ascospore but require the meeting of mycelia developed from different ascospores and then not from any two but from two of opposite sexual strains. On the other hand some species of *Ascobolus* are fertile when grown from but a single ascospore. This is a phase of investigation that is attracting the attention of students but very much still remains to be found out. Drayton has demonstrated that in *Sclerotinia gladioli* there are formed on the mycelium arising from one ascospore minute cells (microconidia or sperms) and certain receptive structures within which arise ascogonia with long trichogynes. Such mycelium remains without producing apothecia. The mycelia produced by the eight ascospores of an ascus represent two phases, four of each. The sperms (microconidia) from any mycelium of one phase can fertilize the receptive bodies of a mycelium of the other phase and vice versa. This is apparently not true heterothallism or condition of maleness and femaleness of the different strains such as occurs among the Mucorales. It is comparable to the self-sterility of many flowering plants to their own pollen, e.g. the Bartlett pear pistil rarely develops to a fruit when pollenized by pollen from the same variety and the same is true for the Kieffer pear, but these two varieties are mutually fertile to each other's pollen. It is perhaps still better comparable to the dimorphic

species of *Primula* studied by Darwin, in which the seeds of a capsule will produce about equal numbers of the two types of primrose plants, those with flowers possessing a long style and low placed stamens and those whose flowers have short styles and stamens high in the corolla tube. Each strain is relatively sterile with pollen from plants of its own type but fertile with pollen from plants of the other type. Whether the condition in *Ascobolus magnificus* is like the foregoing, i.e. a case of self sterility, or is true heterothallism (i.e. real difference in sex) remains to be discovered by further study.

The "Discomycetes" were classified by the earlier investigators, Persoon and Fries, largely on the basis of external characters. Later the ascus and ascospore characters were also taken into consideration. The internal structure of the apothecium showed itself to be of great importance. Durand used this as a basis for a tentative classification. Nannfeldt has used these features in his extensive writings on this group. Boudier pointed out that the mode of dehiscence of the ascus, whether by a lid or by a pore, i.e. operculate or inoperculate asci, is of great diagnostic value. Seaver in his recent volume on the Operculate Cup-fungi recognizes only two families in place of a larger number recognized by Lindau in Engler and Prantl.

Order Pezizales: Operculate Forms.

FAMILY PEZIZACEAE.—Apothecia flat, convex or concave or cup-like, sessile or short stalked, rarely long stalked and then the hymenium concave (or at most flat). Apothecium pseudoparenchymatous throughout with few exceptions.

Typical representative genera in this family are: *Ascobolus* (Figure 51, I), growing on animal excrement or on soil, with mature asci much protruding, and with mature spores violet. The apothecia vary, according to species and environment, from less than 1 mm. up to nearly 3 cm. in diameter. In *A. immersus* the ascospores may attain a size of 50–75 μ in length by 20–35 μ in thickness. *Pyronema*, growing on soil, especially after a fire or after steaming. The apothecia are 1 to 2 mm. in diameter and the hymenium is practically naked from the first. The ascospores are hyaline. *Humarina* (= *Humaria* Sacc.) less than 1 mm. to 1 cm. in diameter, growing on the ground, forming white or bright colored mostly disk-shaped apothecia, with hyaline ascospores, differing from *Ascophanus* only in that the latter grows on dung. *Patella*, with disk-shaped apo-

thecia up to 1 cm. wide, and with the outside clothed with hairs, at least at the edge. *Patella scutellata* (*Lachnea scutellata*) forms its brilliant red disks with a fringe of dark hairs on rotten wood and is strikingly beautiful. *Plectania* (= *Sarcoscypha*) has stipitate apothecia growing on sticks lying on or buried in the ground. Its

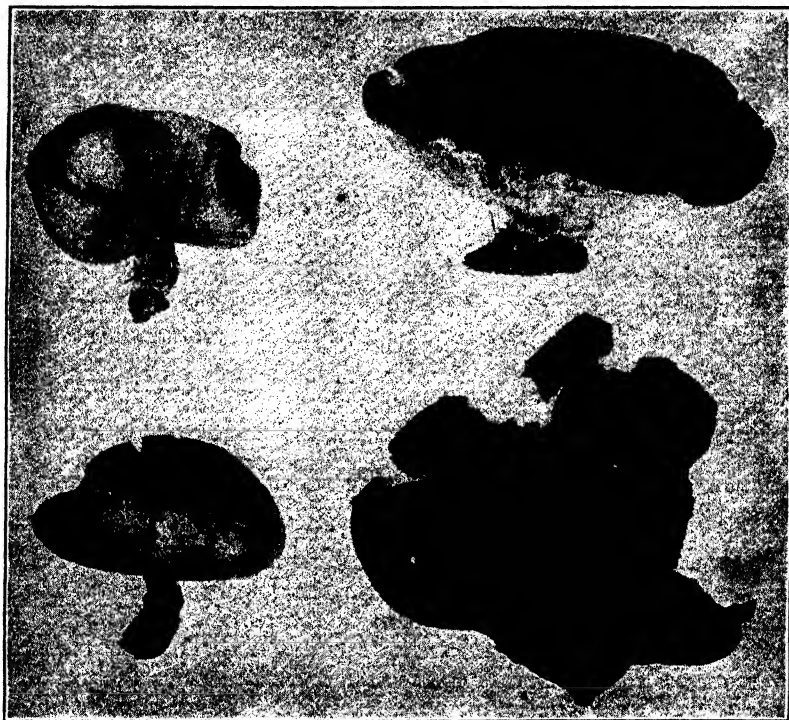


FIG. 52.—Pezizales. *Peziza venosa*. (Original, F. C. Strong.)

hymenial surface is brilliantly colored. *P. coccinea* is very abundant in some regions in early spring forming apothecia sometimes 3 or more centimeters in diameter. The stipe is buried in the soil. *Peziza*, with saucer to cup-like apothecia, usually of considerable size, 2 cm. up to 30-40 cm. *Peziza badia* and *P. venosa* (Figure 52) are quite frequent in woods and *P. vesiculosa* in greenhouse soil that has been heavily manured.

FAMILY ELVELACEAE (= *Helvellaceae*).—Apothecia stalked, convex, attached at the apex of the stalk or grown fast to its upper portion.

To be mentioned are *Elvela* (= *Helvella*), with the apothecium more or less saddle-shaped, attached by the center of the under side of the saddle (Figure 53). The hymenial surface may be smooth or gyrosely folded. *Morchella* with the apothecium grown fast down the side of the upper part of the stalk and with its surface thrown into strong longitudinal and transverse folds so as to be coarsely pitted, thus greatly increasing the hymenial surface. The species of this genus are known as Morels or Sponge Mushrooms and are among

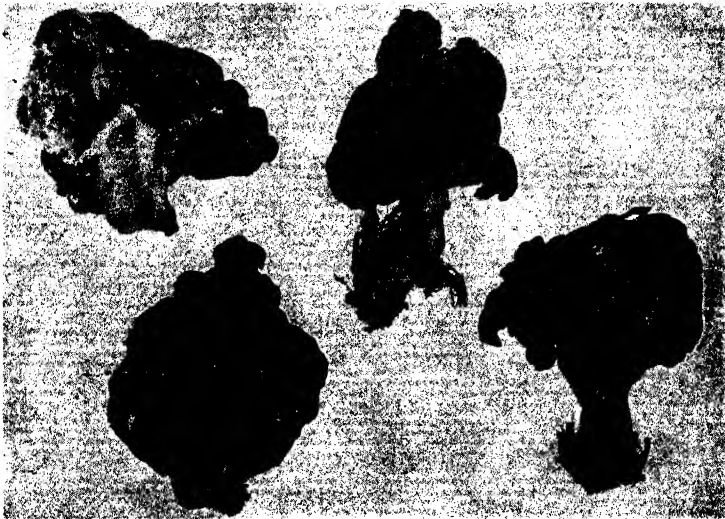


FIG. 53.—Pezizales. *Elvela infula*. (Original, F. C. Strong.)

the most delicious edible fungi known (Figure 54). They grow mostly in deciduous woods, fruiting in the spring. *Verpa*, the Bell Morel, has the cap shaped like a bell and free from the stalk. It may be smooth or longitudinally ribbed externally. It is edible, coming a little earlier than the true morels.

Order Pezizales: Inoperculate Forms.—Nannfeldt separates the inoperculate apothecial fungi into three orders, distinct from the Pezizales, viz. Lecanorales, Ostropales and Helotiales. The first are with few exceptions lichen-forming fungi, those that do not have this habit being considered as being descended from such forms. The other two orders are saprophytic or parasitic on higher plants, not forming lichens. The Ostropales include one family

with strong apical thickening of the ascus and thread-like ascospores. The Helotiales contain the majority of genera and consist of forms with asci only slightly thickened apically and with spherical to elongated, in one family almost needle-shaped spores. The apothecia are frequently formed upon or within a stroma or this may be found



FIG. 54.—Pezizales. *Morchella conica*. (Original, F. C. Strong.)

only at the upper side of the apothecium. Nannfeldt divides this order provisionally into six families one or more of which include the genera usually included in the Order Phacidiales which he gives up entirely. The author follows Nannfeldt in the main in the following discussion although recognizing that much more work must be done before it can be said that we really know well the interrelationships of these fungi. He, however, includes these families within

the limits of the Order Pezizales until such time as more complete knowledge will justify breaking the Lecanorales and Pezizales into several orders accompanied by a redistribution of the families. Not all of the families recognized by Nannfeldt are mentioned below.

FAMILY HELOTIACEAE.—Apothecia disk or cup-shaped, at first closed, often stalked, the tissues below the hymenium, i.e. the excipulum, of filamentous hyphae sometimes grading into an outer layer of shorter, thicker cells. Mostly saprophytes or parasites on plant tissues. *Chlorosplenium aeruginosum* occurs on wood and stains it a distinct green. *Sclerotinia* produces extensive mycelium

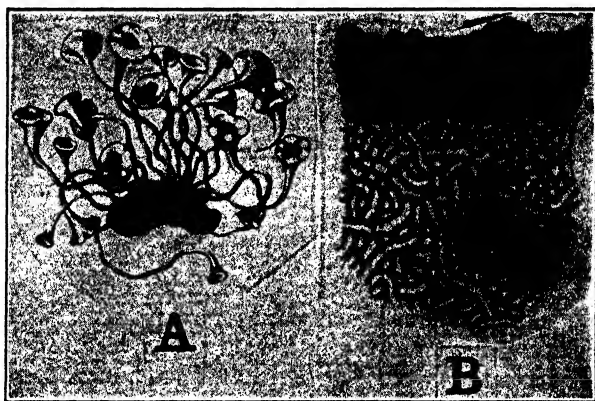


FIG. 55.—Pezizales. *Sclerotinia sclerotiorum*. A, apothecia growing from sclerotium; B, magnified section of sclerotium. (After Brefeld, 1881.)

which may in some species grow saprophytically, but is capable of being destructively parasitic. It forms sclerotia varying from a few millimeters up to two or more centimeters in diameter. Out of these grow the frequently stalked apothecia (Figure 55, A, B). Many species have extensive conidial formation, either *Monilia* like (species attacking stone and pome fruits and assigned to the genus *Monilinia* by Honey) or *Botrytis* like. The species *S. sclerotiorum* produces no germinable conidia but numerous microconidia which possibly have the same function as those of *S. gladioli*. *Trichoscyphella* (*Dasyscypha* of some authors) forms sessile apothecia parasitic upon conifers, some species causing serious damage, e.g. *T. willkommii* causing cankers on *Larix*. *Helotium* produces sessile or almost sessile disk or cup-shaped apothecia on plant parts,

sometimes as saprophytes sometimes as parasites. The ascospores eventually are 2 to 4 celled.

FAMILY MOLLISACEAE (*Dermateaceae* in part according to Nannfeldt).—This differs from the foregoing family in having a distinct pseudoparenchymatous excipulum of mostly thick and dark-walled cells. The species are to a large extent parasitic on plant parts, often formed within the host tissues and breaking out at maturity of the apothecium.

Mollisia produces its apothecium externally on the host tissues. It has one-celled rather elongated ascospores. *Pseudopeziza*

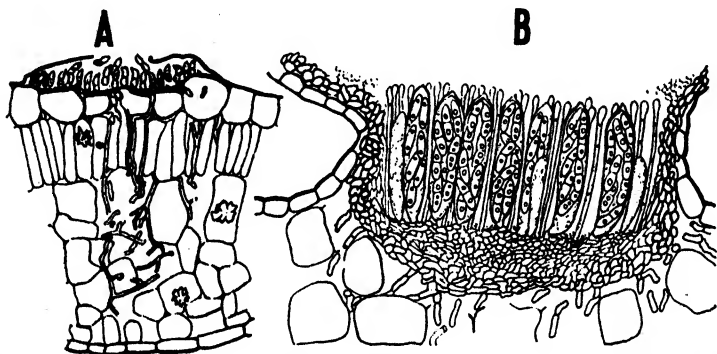


FIG. 56.—Pezizales. *Diplocarpon earlianum*. A, asexual *Marssonina* stage of reproduction; B, section through apothecium. (After Wolf, 1924.)

produces its apothecia out of a well developed stroma under the epidermis of the parasitized leaf which is ruptured at the maturity of the apothecium. The ascospores are 1-celled. *Ps. medicaginis* is sometimes the cause of yellowing of the foliage of alfalfa or lucerne (*Medicago sativa*) and premature leaf-fall. *Ps. ribis* (*Drepanopeziza ribis*) produces its apothecia on the dead leaves of species of *Ribes*. The actively parasitic stage of the fungus produces only the conidial type of reproduction formerly known as *Gloeosporium ribis*. *Diplocarpon* (Figure 56) likewise produces its apothecia upon dead leaves sometimes under a superficial radially arranged shield-like stroma sometimes not. The parasitic stage produces the conidial form known as *Actinonema* when the radiating dark hyphae are present or *Marssonina* (Figure 56, A) in their absence or *Entomosporium* when the conidia have hair-like appendages. *Higginsia* Nannfeldt includes those forms formerly called *Coccomyces* whose conidia in

stage forms the genus *Cylindrosporium*. Some species of *Higginsia* are of great economic importance, causing "yellows" or "shot-hole disease" of species of *Prunus*. The elongated conidia are formed subepidermally in an acervulus. Later in the summer in the same or other acervuli small almost spherical cells are formed, frequently called microconidia. In a stroma developing below the acervulus Higgins and also Backus observed the formation of numerous elongated coiled ascogonia which extend up to the microconidial layer. Backus has demonstrated that these microconidia grow fast to the terminal cells of the ascogonium, i.e. to the trichogyne, and should therefore be considered as sperm cells. Subsequently the ascogenous hyphae are produced and the apothecium develops.

FAMILY PHACIDIACEAE.—The apothecia of this family arise in a well-developed stroma which encloses it below and above, and which is often lenticular in vertical section. These stromata may be superficial or buried in the tissues of the host plant. Possibly as a result of the protection afforded by the stromatic envelope the excipulum is not strongly developed. The stromata may be rounded or elongated. In the former case the stromatic cover often splits stellately at maturity to reveal the apothecium, while in the elongated forms a longitudinal slit is formed. There may be but one apothecium in a stroma or several. In the latter case each apothecium may be elongated more or less, even when the stroma is isodiametric. The asci are clavate with hyaline, filamentous paraphyses. The ascospores are shot off as in the Pezizaceae when the mature hymenium is exposed by the opening of the stromatic cover. They are elongated and sometimes needle-shaped, one to many celled, hyaline or colored. They often have a gummy outer layer. Asexual reproduction is known for many species. These conidial forms usually belong to the form family Leptostromataceae of the Fungi Imperfecti. Some species are saprophytic but perhaps the majority are parasitic upon leaves or twigs.

Phacidium possesses a circular stellately dehiscing stroma with a single apothecium. *P. lacerum* occurs on the needles of *Pinus silvestris*. Several species of *Lophodermium* also attack needles of Conifers, causing serious leaf fall. In this genus the stroma as in *Phacidium* contains only a single apothecium, but both stroma and apothecium are elongated and narrow, and the dehiscence is by means of an elongated slit. *Rhytisma*, the cause of the tar spot of

leaves of maple (*Acer*) and other plants produces a large more or less isodiametric subcuticular stroma on the upper side of the leaf and usually a smaller sterile stroma on the under side. After leaf fall the apothecia begin to develop slowly but do not reach maturity until the following spring. In a single stroma are produced numerous elongated apothecia. These do not lie strictly parallel but are more or less sinuately curved or sometimes rather radiately arranged.

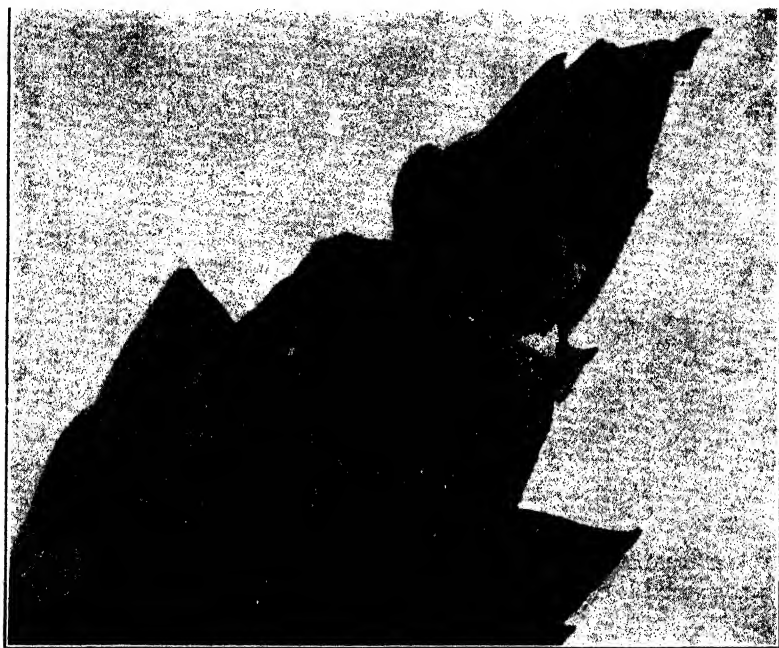


FIG. 57.—Pezizales. *Rhytisma acerinum*. (Original, F. C. Strong.)

At maturity the stroma forms a slit over each apothecium which under proper moisture conditions pulls back at the sides so that the hymenium is fully exposed (Figure 57). At least three species occur on various species of *Acer*, each showing a narrow specialization to only one host or to a group of host species. The red maple (*Acer rubrum*) is very subject to the disease in some parts of North America. S. G. Jones has shown that in the stroma there arise ascogonia, at first one or two celled which become 3 to 5 celled. The cross walls become perforated and almost completely absorbed and the nuclei pass into one of the central cells, the ocyone, from

which arise the ascogenous hyphae with numerous pairs of nuclei. No nuclear fusion occurs until in the young asci which are formed by the hook method.

FAMILY GEOGLOSSACEAE.—This family was formerly associated with the Elvelaceae to form the Order Elvelales, before the importance of the type of dehiscence of the asci became apparent. The apothecium is stipitate and the hymenium either forms a closely adherent layer to the somewhat thickened upper part of the stipe or forms the upper surface of a head borne at the apex of the stipe. The spore fruit may be entirely made up of hyphae or the cortex may be pseudoparenchymatous. In spite of the external position of the mature hymenium it is really formed endogenously, being covered when young by a distinct veil as in most other genera of the Pezizales with convex hymenium. The ascospores are ellipsoid and 1 or 2 celled (*Mitrella*) or long elliptical to filiform and several to many septate. They are hyaline to smoky to dark brown in color. In a few species the spores bud into innumerable small spores while still within the ascus. The fruiting bodies vary from a few millimeters to 5 or more centimeters in height. They are mostly found on rotten wood, decaying leaves, moss or soil, usually where plenty of moisture is available, in one species submerged in running water. Several genera have bright colored spore fruits (e.g. *Mitrella*, *Spathularia*, etc.) while those of others are black (e.g. *Geoglossum*). The following genera are worth mentioning: *Mitrella*, spore fruit clavate, bright colored, ascospores hyaline, ellipsoid; *Microglossum*, similar but with ascospores elongated and

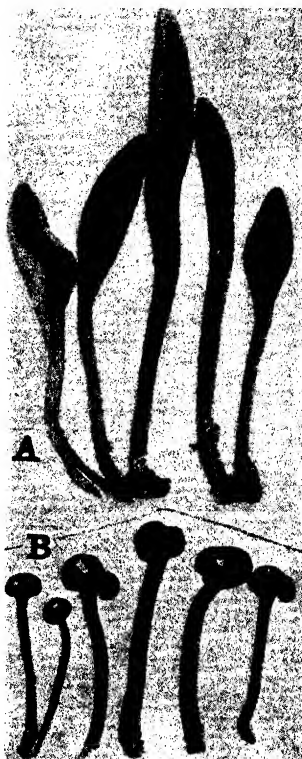


FIG. 58.—Pezizales, Geoglossaceae. A, *Geoglossum glabrum*; B, *Leotia chlorocephala*. (After Durand, 1908.)

many septate; *Geoglossum* (Figure 58, *A*), clavate, black, smooth and dry, ascospores dark, many septate; *Gloeoglossum*, similar but viscid-gelatinous; *Trichoglossum*, similar to *Geoglossum* but beset with spines or setae; *Spathularia*, fan shaped, bright colored, ascospores hyaline, many septate; *Leotia* (Figure 58, *B*), spore fruit capitate, gelatinous, spores narrowly ellipsoid; *Cudonia*, capitate, leathery, ascospores filiform, multiseptate. Eleven genera and about 41 species are recognized from North America by Durand in his excellent monograph of the family.

FAMILY CYTTARIACEAE.—The position of this family is not certain, though it probably should be included in the Pezizales. It is not closely related to any of the foregoing families. Apothecia numer-

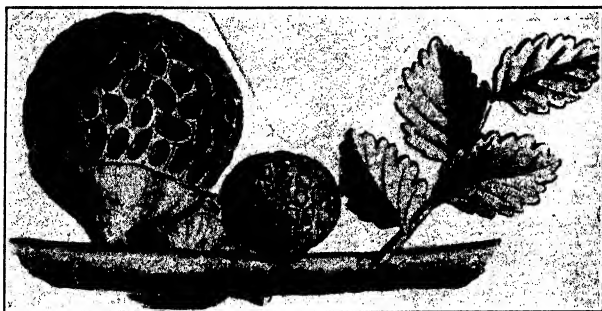


FIG. 59.—Pezizales. *Cyttaria gunnii*. (After Lindau in Engler and Prantl, 1897.)

ous, imbedded in a fleshy stroma produced externally on the twigs of the host. Ascospores 1-celled, hyaline. One genus, *Cyttaria*, confined with its hosts (species of *Nothofagus*, the Southern Beech) to the South Temperate Zone in South America and Australasia (Figure 59). The fleshy stromata serve the natives as food. The basal portion of the stroma of one or more species produces organs resembling spermatophytes with sperm cells.

Order Tuberales.—The fungi of this order are all terrestrial and produce subterranean spore-fruits (ascocarps). Some are probably saprophytic but it seems possible that certain species are perhaps parasites upon the roots of higher plants. The ascocarps vary in diameter from a few millimeters up to three or more centimeters and may be found close to the surface of the soil or at a considerable depth. With no direct means of bringing the ascospores

into the air for distribution by air currents as is the case in the Pezizales, the Tuberales depend for their distribution largely upon the activities of mycophagous animals, probably to a considerable extent insects, but, for some species at least, ground-inhabiting rodents. Thus in California the so-called ground squirrels dig out the fruiting bodies, doubtless attracted by the odor diffusing up through the soil, and eat them on the spot or carry them away to their burrows or other hiding places. In these processes pieces of the ascocarps are scattered and the ascospores find their way into the soil. By germination of the ascospores of one species of *Tuber* a conidium-bearing mycelium has been obtained but this has never been grown to the stage where the ascocarps were produced.

The sexual process is unknown in the Tuberales, the hypogaeous habitat of the fruiting body making it very unlikely that it would be observed except by very rare accident. The structure of the immature spore-fruit has been studied in a good many cases but for many species only the mature ascocarps are known. By comparing these mature stages, taking cognizance of the ontogeny of the ascocarp where it has been observed, Fischer and also Bucholtz recognized a graded series leading from types scarcely different from some of the Pezizales that have almost completely subterranean apothecia to very complex forms such as those of *Tuber* in which the apothecial nature of the ascocarp is almost entirely concealed.

Perhaps the simplest structure is that found in some species of the genus *Genea*. This develops as a closed apothecium which opens fairly wide at maturity. The inner surface is occupied by a hymenium consisting of almost cylindrical, eight-spored asci and slender paraphyses which overtop the asci, thus forming an epithecium. This may consist of only the swollen tips of the paraphyses, meeting above the asci, or may be further developed into a thick pseudo-parenchymatous layer. The hymenium may be even or may be thrown into folds which divide the apothecial cavity into chambers opening into a common cavity near the external opening. The edges of these folds may be sterile so that the hymenium is formed only on the surfaces lining the smaller chambers which may, themselves, be thrown into folds. In *Hydnотria* these chambers with their folded hymenial surfaces connect separately to the exterior at many points instead of through one common opening. Sometimes the epithecial development is continuous throughout the chamber,

filling it with a loose tissue. This is the case in *Pachyphloeus* which resembles a *Genea* with folded hymenium and one external opening, except that the epithecium fills the whole cavity of the apothecium with a pseudoparenchymatous tissue. In *Tuber* (Figure 60) there may be but one series or several series of passages, the passages and chambers being filled with the pseudoparenchymatous growth. In this genus the asci are ovoid or spherical and often but few spored.

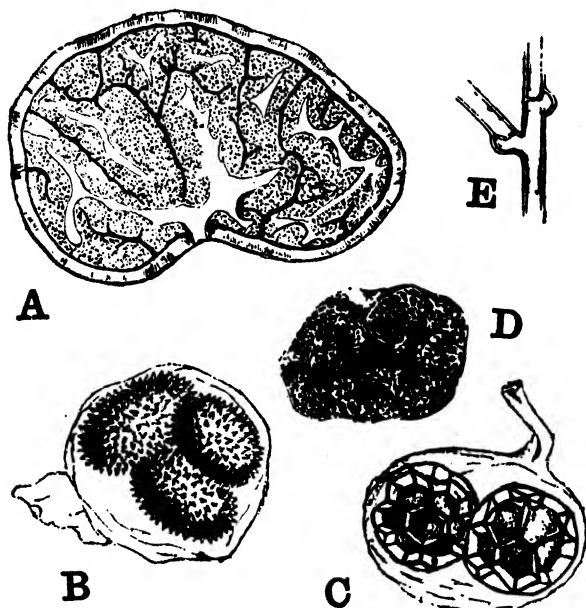


FIG. 60.—Tuberales. A, vertical section through *Tuber rufum*; B, ascus of *T. brumale*; C, ascus of *T. magnatum*; D, *T. lapideum*; E, clamp connection on mycelial strand growing out of ascocarp of *T. lapideum*. (A–C after Tulasne, 1851; D–E after Mattirollo, 1888.)

They do not form a single hymenial layer but project into the epithelial tissues at various levels. A number of other genera are recognized with varying degrees of modification of the foregoing structural types. Of all of the species of the order a few species of the genus *Tuber* (the truffle) are of economic importance. These species, especially *T. aestivum* and *T. melanocarpum*, occur in the rather open forests of Southern Europe (mainly under species of *Quercus*), where they are collected by the use of trained animals (dogs or pigs) which find them by their odor. In recent years many

species of Tuberales have been discovered in California where the climate is quite similar to the regions of Europe where they are best known.

Order Hysteriales.—In this order of plant-inhabiting saprophytes and parasites the apothecia are much reduced in size and compressed laterally to elongated, often somewhat boat-shaped structures, opening by a long narrow slit. They are dark colored, leathery or hard and show a strong contrast between the dark-

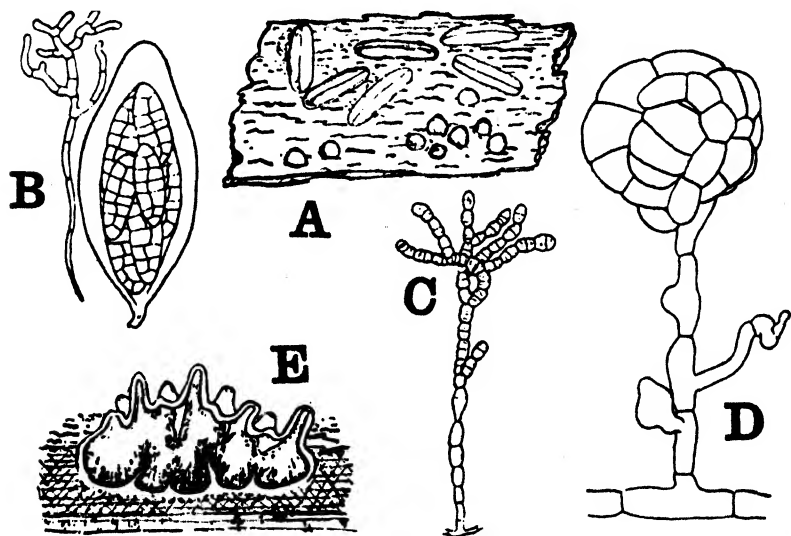


FIG. 61.—Hysteriales. A, *Hysteroglyphium minutum*, apothecia; B, ascus and paraphysis; C, asexual (*Septonema spilomeum*) stage of *Hysterium insidens*; D, asexual (*Papulospora mytilina*) stage of *Lophium mytilinum*; E, asexual (pycnidial) stage of *Lophium mytilinum*. (After Lohman, 1933.)

colored, hypothecium and the light-colored hymenial layer. The latter consists of ovoid to elongated-cylindrical asci intermingled with mostly septate paraphyses which are frequently enlarged at the apex or branched (Figure 61, B), even forming at times a well marked epithecium. The apothecia may be single or in closely packed groups, superficial or buried in the substratum which in that case also tears when the apothecium opens. The asci open by a pore, not by a lid. The ascospores are of very many different forms, as in the Phacidiaceae, to which this order shows many points of relationship. They are ellipsoid and one-celled, or several celled

or divided both longitudinally and transversely into many cells (Figure 61, *B*), or needle shaped. In color they vary from hyaline to brown. Conidial formation has been reported in a few species, usually with the conidiophores included in a pycnidium or somewhat similar structure. Lohman has shown that some of the conidial forms usually assigned to the genus *Sporodesmium*, of the Fungi Imperfecti, are the conidial stages of certain species of Hysteriales. Besides this spore form other conidial stages observed by him represent the genus *Papulospora* (Figure 61, *D*) and *Septonema* (Figure 61, *C*) of the Moniliales and various forms of the Sphaeropsidales (Figure 61, *E*). The details of sexual reproduction are almost unknown in this group. The relationships within the order and to other orders are still more or less problematical. Usually the over 400 species are divided among several families. Of these Nannfeldt removes the genera assigned to the Family Hypodermataceae to the Phacidiaceae, where they have been given place in this work. This leaves as the only important family the Hysteriaceae.

FAMILY HYSTERIACEAE.—Apothecia external, black and carbonaceous, single or united in a stroma. Most of the species of this family are saprophytic on bark or decorticated twigs or branches (Figure 61, *A*). *Hysterographium fraxini* is common on various species of ash (*Fraxinus*). Its ascospores are dark colored and divided by many transverse and longitudinal septa. The apothecia are boat shaped. Some of the leaf-inhabiting fungi formerly ascribed to this order (e.g. the genus *Parmularia*) are placed by the more recent students of the group in the Pseudosphaeriales.

The relationship of this order is more or less in dispute. The compact hymenium with numerous well developed paraphyses and the slit-like opening show great affinity to some of the Phacidiaceae as does the great variability of ascospore structure. The suggested relationship to the Family Lophiostomataceae in the Order Sphaeriales seems doubtful, in spite of the slit-like ostiole, for in other respects the Lophiostomataceae are typically Sphaeriaceous.

Order Taphrinales (Exoascales).—This is a group of fewer than 100 recognized species of fungi, all but a very few parasitic. Two or more genera are recognized in two families whose actual relationship to one another is uncertain in the absence of developmental studies in one of these families. Both families are characterized by the production of a superficial hymenium with indeterminate

margin and without paraphyses. This may rest upon a thin membranous hypothecium consisting of interwoven hyphae (*Family Ascocorticiaceae*) or may burst through the epidermis or cuticle of the host plant without definite hypothecium (*Family Taphrinaceae*). In the author's opinion these represent the ultimate steps in the reduction and simplification of an apothecium. Together with this simplification of apothecial structure there has arisen a marked modification of the sexual process in the Taphrinaceae (no studies on this point being recorded for the Family Ascocorticiaceae). According to Miss Wieben, the life history for *Taphrina epiphylla* and *T. klebahnii* is as follows: An ascospore, or one of the smaller spores which the ascospores produce by budding while still within the ascus, germinates upon the surface of the host plant. Only when the germ tubes from two such spores of opposite sexual phase meet and fuse is active infection of the host possible. As a result of this conjugation a dicaryon mycelium arises which grows intercellularly in the host tissues. Fitzpatrick has shown that in *T. deformans*, a single spore can cause infection (Figure 62, *E*). The nucleus of this spore divides and thenceforth the two nuclei divide conjugately and the vegetative mycelium is of dicaryon nature as in the case of the species studied by Miss Wieben.

The presence of these hyphae causes hypertrophy and hyperplasia in the affected parts of the host. This may affect the leaves, fruits and shoots, often causing the formation of "witches' brooms." Eventually dicaryon cells are formed at the surface of the host, often in a subcuticular location, forming a structure resembling pavement epithelium (Figure 62, *D*). These cells sometimes become somewhat thick-walled. In them eventually nuclear fusion occurs, followed by elongation of the cell in a vertical direction, rupturing the cuticle (Figure 62, *A*). The diploid nucleus and most of the cytoplasm pass into the upper part of the cell leaving an empty lower part which is sometimes but not always cut off from the upper part by a cross wall. The diploid nucleus now undergoes meiotic and mitotic division, the spindle of the first division being transverse, according to Juel. Around the eight nuclei thus formed the ascospores develop (Figure 62, *B*). In many species each ascospore undergoes budding so that the ascus becomes polysporous (Figure 62, *C*). Wieben's germination experiments have shown that four of the ascospores (and the spores produced from them

by budding) are of one sexual phase and four of the other, but in *T. deformans* this distinction does not occur.

Lohwag advances reasons for believing that *Taphrina* is not a true Ascomycete but a Basidiomycete which has reverted to the ancestral condition. The normal basidium, in his viewpoint, represents an ascus in which the ascospores have pushed out into a projection of the ascus wall so as to become apparently external,

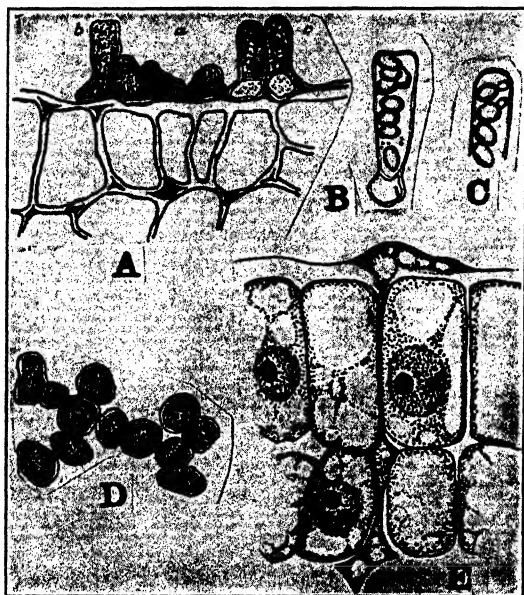


FIG. 62.—Taphrinales. *Taphrina deformans*. A, section of leaf showing asci in various degrees of development; B, mature ascus showing empty basal portion; C, portion of ascus showing two ascospores beginning to bud; D, subcuticular ascogenous cells seen from above; E, infection of leaf by dicaryon mycelium. (A–D after Pierce, 1900; E after Fitzpatrick, 1934).

although really still within the wall. In *Taphrina* the transverse position of the nuclear spindle, the habit of budding on the part of the ascospores, and the parietal position assumed by the ascospore nuclei before the spores are delimited are all pointed to as Basidiomycetous characters.

Ascocorticium, the only genus of the FAMILY ASCOCORTICIACEAE consists of a small number of species whose fructifications produce a gray or pink colored, thin coating with indeterminate growth, over the surface of bark of dead trees. The hypothecium consists of 4

to 6 layers of interwoven hyphae running parallel to the surface of the bark. Upon these arise the ovoid 8-spored asci. The nuclear phenomena accompanying the ascus formation have not been studied and it is not known whether there is any sexual process other than the probable union of two nuclei in each young ascus.

Taphrina (*Exoascus*, *Magnusiella* or *Taphria*) is the only genus of the TAPHRINACEAE. Of great economic importance is *T. deformans*, causing the disease of the peach (*Amygdalus persica*) known as leaf curl. The ascospores or spores arising from them by budding lie dormant in crevices of the twigs or on the bud scales until the following spring when they germinate and infect the young leaves and even the fruits and young twigs. The affected leaves become much thickened and distorted as well as discolored. The diseased fruits may show irregular bright red patches of thickened tissues. On the diseased areas the asci are formed subcuticularly in the late spring or early summer. In a few cases the spores appear to germinate soon after formation so that Waite and Poole report what may be a secondary infection occurring the same season. *Taphrina pruni* infects the young fruits of *Prunus* and *Padus*, causing them to develop into the hollow hypertrophied structures which, upon the plum, are known as "plum pockets." The asci here also are subcuticular. *T. cerasi* causes witches' broom on various species of cherry (*Prunus cerasus*, *P. avium*). The mycelium lives perennially in the tissues of the host. *T. alnitorqua* causes hypertrophy of the scales of the aments of the alder (*Alnus*). In *T. potentillae* the mycelium lives beneath the epidermis and sends up, between the epidermal cells, branches which bear separate asci.

In this family the whole vegetative mycelium consists of dicaryon cells and is therefore comparable to the ascogenous hyphae of those forms with definite sexual organs and well developed apothecia, such as *Pyronema*, etc. Many authors consider this family to be primitive but it seems more logical to consider it as a much simplified offshoot of the Pezizales, the Ascocortiaceae being a possible intermediate stage.

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CHAPTER VIII

CLASS ASCOMYCETEA: THE "PYRENOMYCETES"

With the exception of the Order Laboulbeniales the Ascomyceteae so far considered have been those whose spore fruits are apothecia or modifications of apothecia. In this chapter will be discussed those orders which produce true perithecia with ostioles, or stromata containing cavities within which the asci are developed. Because the life histories of all but a few of these thousands of species are entirely unknown the relationships of these orders to one another and of the genera within the orders are admittedly very uncertain. Indeed, with further study it is almost certain that the limits of the orders will have to undergo radical revision. For this reason a rather conservative attitude is taken as to these groups. The author does not believe that the true relationships are shown by the arrangement chosen, but this is due to the ignorance of the ontogeny of the species of so many of the groups.

Whether logically the perithecial forms should be treated after or before the apothecial forms is a matter of convenience rather than of expression of phylogenetic history. It seems likely that very early in the origin of the Ascomyceteae three tendencies began to be emphasized. In the one the female sexual branch bore an oogone surrounded with a protective layer, as in many Florideae; this group led to the Laboulbeniales. In the two other series the female sexual organs were naked. In the one the number of the ascogenous hyphae and their branches was great and a rather wide spreading spore fruit developed, the apothecial series of fungi; in the other the ascogenous hyphae were short and usually few, little branching if at all, and the protective structure formed about them (the perithecium) remained small. So far we have followed the first two series of development, we now return to the relatively primitive forms again and start to follow the third series. It should be noted that the basal groups of each of these series include forms with free, non-motile sperms which come in contact with some receptive structure (trichogyne) and thus

bring about fertilization. In the apothecial series as well as in the perithecial series now about to be studied this gives place quickly to the direct union of trichogyne and antherid and finally to the entire disappearance of the trichogyne, and in many cases of the antherid.

In all but the more recent works but three orders are recognized in which typical ostiolate perithecia are produced, and several other orders in which the perithecia have been modified in various manners, including eventually the loss of the ostiole. These orders with ostiolate perithecia are the lichenogenous Pyrenulales, and the non-lichenogenous Sphaeriales, both with dark perithecia, and the Hypocreales with light colored, usually more or less soft perithecia. The possible interrelationships will be taken up in the discussion of these orders. These orders as customarily limited include many fungi with perithecium-like structures which prove upon closer examination and, particularly, upon study of their ontogeny to be really stromata with the asci produced in cavities which lack true perithecial walls. The true perithecial wall arises from the cells that support the ascogonium and antherid (if present) and by outward and upward growth produce a hollow body within which the ascogenous hyphae may spread. From the inner surface of the wall grow the paraphyses which intermingle with the asci while near the apex the periphyses by their further upward growth assist the apical cells of the wall to open an ostiole through the stromatic covering which according to Julian Miller apparently is present, at least as a thin layer, in all of these three orders.

Order Sphaeriales.—This order is taken up first, not from any conviction that it is more primitive than the other two but, because in the absence of evidence to the contrary, it offers a better field to point out the various developmental directions in the modification of the perithecia. If, as the author suggested for the Lecanorales, the primitive Ascomyceteae were aquatic and parasitic upon water animals (leading to the Laboulbeniales) or algae, leading to the lichens, we should place the Pyrenulales before the Sphaeriales, but so little is known of their life histories they can best be understood after considering the much better studied Sphaeriales.

The various modifications in the perithecium will be taken up first, then the little that is known as to the details of the sexual reproduction. In this order, more than in any other order of the

Ascomyceteae the classification into families and genera needs thorough-going revision based upon careful studies of the life histories. Until that is accomplished in a fairly complete manner the classification must necessarily be based upon the structure of the mature perithecia, which may or may not give a true picture of the relationship.

The perithecial wall is in general dark colored, at least in its outer stromatic layer, pseudoparenchymatous in structure, and free from the enclosed asci which arise from the base or part way up the sides of the perithecium. Sometimes the asci form a dense hymenium such as is found in the apothecium where the closely packed asci give the mutual protection which the enclosing perithecial wall makes unnecessary but frequently they are more loosely arranged. Paraphyses are present, but are usually delicate and evanescent and not very numerous. Periphyses, i.e. paraphysis-like threads at the edge of the hymenium but not intermingled with the asci are much more frequent. The asci may reach maturity at different ages within the perithecium, a phenomenon not rare in the apothecial forms also. The ascospores may be expelled violently through a pore (not a lid or operculum) at the apex of the ascus or the osmotic pressure within may rupture the ascus at its middle so that the upper half is forced off or the outer layer may break at the apex and contract, allowing the inner layer to expand and finally burst, or the asci, paraphyses, etc., may be digested within the perithecium leaving the ascospores imbedded in a gummy mass which absorbs water during a rain and swells, emerging from the ostiole, where the gum is dissolved away and the spores carried off by the currents in the film of rain water or splashed off in the droplets caused by the striking rain drops. In some genera only the ascus stalk digests, the resultant gummy mass containing the unchanged bodies of the asci. The asci vary from cylindrical to club-shaped or obovate, sometimes being drawn out below into a narrow stalk-like portion. The ascospores may lie in one or more rows or in a ball-like cluster in the ascus. The number is mostly 8 but in a few cases only 4 spores are formed and in others 16 to 32 or even as many as 256 or 512 are reported. They vary exceedingly in size, shape, structure and color. They may be colored or hyaline, 1 celled, 2 celled, several celled in one row (i.e. phragmosporous), many celled by both cross and longitudinal walls (i.e. muriform), long and slender, or even tetra-

hedral. The recurrence of certain spore and ascus types in what the current classifications consider to be widely distant families has led (and probably rightly) some mycologists (e.g. Vincens, Julian Miller, von Höhnelt, Wehmeyer and others) to attempt to amend the classification so as to bring together those forms with similar asci and spores.

Asexual reproduction probably reaches its highest degree of development in this and the following orders. A very large proportion of the species have asexual reproduction by means of conidia. The types of conidial production are most varied. In many cases perithecial production is relatively rare, the conidia serving to maintain the species. In many of the parasitic species the asexual mode of reproduction alone occurs on the living host and the perithecia are formed only on the dead host tissues. The conidia may be produced on free conidiophores or on conidiophores crowded in an acervulus or on conidiophores enclosed within a pycnidium. In some cases all these forms occur in the same species of fungus in different stages of growth. Judging by the types of asexual reproduction perhaps the majority of the so-called Imperfect Fungi (Class Fungi Imperfecti) are probably conidial stages of this and closely related orders, although possibly representing in many cases species that have permanently lost their power of sexual reproduction.

Studies have been made of the sexual reproduction in various forms of the order, but not only are there great numbers of genera in which studies are lacking, but for many families, even, no such studies have been made. The results are conflicting for some of the supposedly closely related forms. In these usually difficultly sectioned and stained organisms, often with many stages missed during the investigation, the previously held views unconsciously affect the interpretation of the things seen. Thus one school of mycologists has always failed to find functional antherids in this and closely related orders, as well as in the Lecanorales and Pezizales. Others report the passage of nuclei from antherid to oogone but deny that these unite in the oogone, insisting that only in the ascus does fusion occur. Still others observe a fusion in the oogone and a second one in the ascus. In view of the contradictory nature of the evidence gathered by students with these different viewpoints it is impossible to decide at present which of these theories is correct, if indeed they may not all be correct, for different organisms within

the class. Still it must be borne in mind that all three viewpoints have been "substantiated" by the three schools of mycologists in the one Discomycetous species *Pyronema confluens*. So in describing the sexual reproduction in the Sphaeriales the author has had to report the findings as reported by the respective investigators.

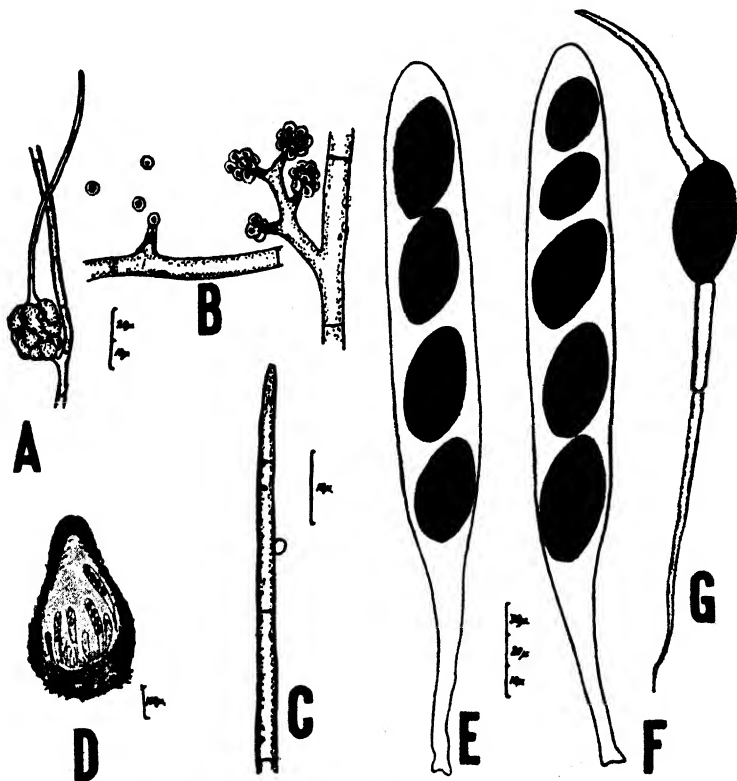


FIG. 63.—Sphaeriales. *Pleurage anserina*. A, ascogonium with trichogyne; B, antherids with sperms; C, trichogyne with adherent, emptied sperm; D, section of perithecium; E, normal ascus; F, abnormal ascus with five spores; G, ascospore, with gelatinous appendages. (After Ames, 1934.)

Until many more forms have been investigated representing all the more important genera and families it will be impossible to determine to what extent weight must be given to this process in the classification of this order.

In the descriptions of sexual reproduction following the author has selected cases from the genera more commonly included in the

Sphaeriales. As will be seen further on some of these forms may belong in other orders. In many of this order spermagonium-like structures are known within which are produced sperm cells like those of *Collema* and *Physcia* in the Lecanorales. In other forms minute sperm like bodies (often called microconidia) have been recorded but are not produced in definite spermagonia. In a great many no such structures have been reported.

Ames found that in *Pleurage anserina* (Figure 63) small flask-shaped antherids are formed out of whose necks the small sperm cells are successively pushed, much as occurs in most of the Laboulbeniales. The ascogonia, produced from the same mycelium consist of coiled structures terminating in slender trichogynes. The fungus occurs in two strains which are self-sterile, but mutually cross-fertile (Figure 64). A sperm cell from one strain placed upon the trichogyne of the opposite strain adheres to it and the contents become emptied into the trichogyne (Figure 63, C). Then there occur growth and multiplication of the cells of the coiled portion and in about four days the perithecium is mature. In a number of other cases forms with trichogyne and sperm cells have been studied but no incontrovertible proof has been offered connecting the latter with the process of fertilization. In two species of *Mycosphaerella* (representing Klebahn's *Septorisphaerella* and *Cercosphaerella*) B. B. Higgins observed the production of minute sperm-like cells in spermagonia and in one case their clustering at the apex of the trichogyne which projected from the epidermis of the dead leaf, but he was unable to detect any direct union of sperm with trichogyne. Later, from the basal portion of the ascogonium arose the ascogenous hyphae. In the author's opinion (perhaps the author is prejudiced) further study will confirm the active function of such sperm-like cells in the majority of cases in which they occur. Many cases are known in which there is a coiled or straight ascogonium of several one to five nucleate cells. The terminal cell may be drawn out into a trichogyne. An antherid may be present coiled about the ascogonium or it may be straight and the ascogonium coiled about it. At their tips they meet and fuse. Passage of the numerous male nuclei from the antherid into the trichogyne has been reported by Killian (Figure 65, B) and by Frey for *Venturia inaequalis* while Elliott reported the passage of one male nucleus from the antherid to the trichogyne in *Ceratostomella fimbriata*. Dangeard

reports the presence of ascogonia but no trace of antherid in species of *Chaetomium*, *Fimetaria*, *Hypocopra* and *Pleurage*. In *Sporormia leporina* Arnold reports that a mycelial cell enlarges and divides, eventually becoming a pseudoparenchymatous body within which a cavity appears, lined by thin-walled cells. From the apex of the cavity long threads grow downward and become enlarged at their

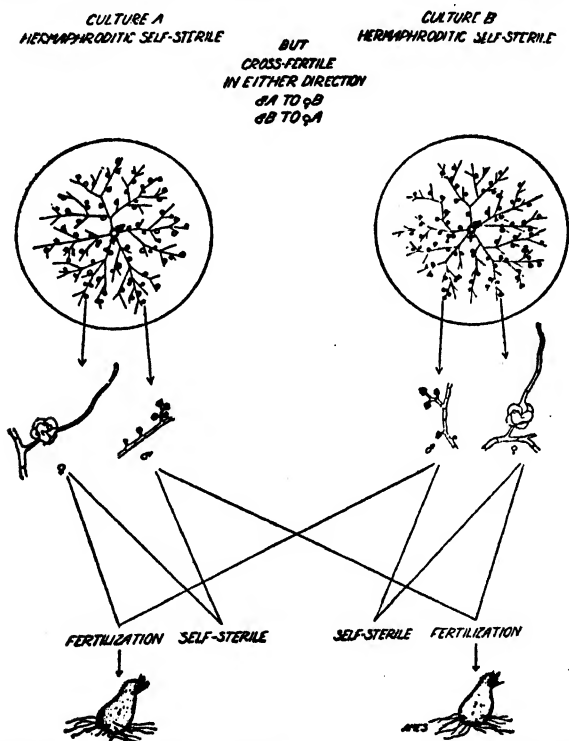


FIG. 64.—Sphaeriales. *Pleurage anserina*; diagrammatic representation of the sexual condition. (After Ames, 1932.)

tips as they approach or reach the floor. There the ascogenous hyphae develop from these enlarged terminal cells and grow up among the descending hyphae, producing asci by the hook method. No true paraphyses are present. From the description and figures it is doubtful whether this is really a true member of the Sphaeriales but rather a stromatic form belonging to the Pseudosphaeriales.

Mittmann, investigating *Ceratostomella fimbriata*, contrary to Elliott's reports failed to find any antherid. The ascogonium begins

as a single, uninucleate somewhat curved terminal cell of a short lateral branch. The cell elongates and coils into several turns, dividing into three to five uninucleate cells. From the supporting cell enveloping hyphae begin to grow which eventually give rise to the perithecial wall. Mittmann suggests that the antherid reported by Elliott was one of these enveloping hyphae. When this envelope

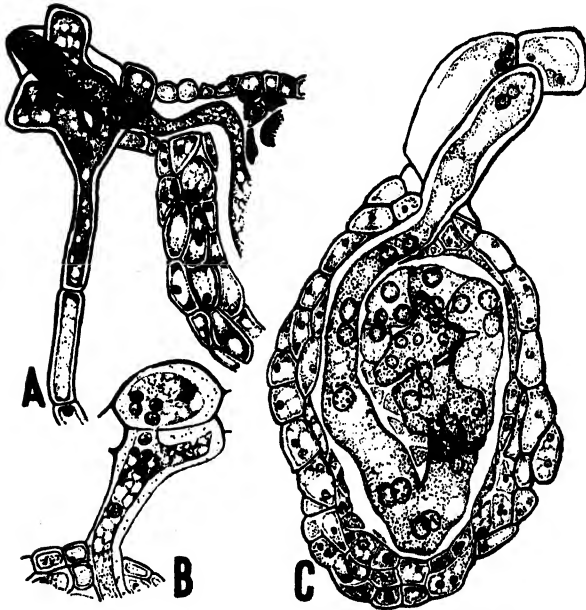


FIG. 65.—Sphaeriales. Sexual reproduction of *Venturia inaequalis*. A, the forked antherid is in contact with the exserted trichogyne; B, sperm nuclei passing from antherid (above) to trichogyne; C, ascogonial cells multinucleate and beginning to form lobes, trichogyne cross walls dissolved out. (After Killian, 1917.)

is several cells in thickness the ascogonial cells enlarge and separate somewhat. One, or sometimes two, of these enlarged cells becomes multinucleate, the number of nuclei usually being eight. This cell (the oogone) divides into several cells which also become 8-nucleate and then divide into binucleate cells which thus form a richly branched system of crowded cells in no definite order. These cells enlarge laterally and their nuclei unite, thus forming the young asci which are nourished by the plasma-rich projecting cells of the inner layer of the perithecial wall. The ascospores are surrounded by a

slime layer. *C. coerulea* and *C. pluriannulata* are reported by Mittmann to be quite similar in development but each falls into two sexual strains, both of which must be present in order that perithecia shall be formed. If Mittmann is correct in reporting that no antherid is present a union of hyphae at some other point seems to be indicated. Sartoris found no antherid near the coiled ascogonium of *C. adiposa* studied by him. Varitchak found in *C. piceae* a non-functional antherid ("trophogone") around which the young ascogonium coiled without uniting with it.

In *Fimetaria* (*Sordaria*) *fimicola* Piehl found the mycelial cells to be plurinucleate. The species is self-fertile. Two hyphae in contact form a connecting opening near the tip by dissolution of their intervening walls. The hyphae begin to coil around one another, one, the female, being larger than the other. Out of the multinucleate threads of the larger thread grow the ascogenous hyphae, the terminal 4-nucleate cell of each of which divides into three cells with respectively 1, 2 and 1 nucleus. These may lie in a straight line or form a hook. The binucleate cell becomes the ascus.

In *Xylaria*, in which numerous perithecia are produced in a stroma, coiled ascogonial hyphae were observed by Brown in the stroma at points where the future perithecia were due to arise, but their further development has not been reported. Somewhat similar structures were reported by Lupo in *Hypoxylon*.

Many of the Sphaeriales lend themselves readily to cultivation on various media. In some cases cultures from single ascospores will produce perithecia, but very often perithecia have not been produced in culture. Edgerton studied a strain of *Glomerella cingulata* in which a scattering development of perithecia was produced on cultures from a single ascospore but yet when two such cultures were allowed to grow into contact with each other in about half the cases (i.e. when the opposite sexual phases met) a great mass of perithecia appeared along this meeting line.

Dowding and also Ames have shown for *Pleurage anserina* as B. O. Dodge showed previously for *Neurospora tetrasperma* that the ascospores are usually four in number and binucleate. From such spores cultures can be obtained which produce perithecia in abundance. Occasionally in place of a binucleate spore two uninucleate spores are produced (Figure 63, E, F). These, Ames has shown,

produce two mutually compatible and self-sterile mycelia while the binucleate spores produce fertile mycelium, each type of mycelium bearing both male and female organs. By cutting off and transplanting hyphal tips containing one or a very few nuclei Ames determined that in the mycelium from the binucleate spores there are two sorts of nuclei which when separated by the hyphal-tip plantings are shown to belong to the two different strains. On this mycelium with both kinds of nuclei some branches produce male and female organs of one phase, self-sterile, and other branches produce similar organs, also self-sterile, but the two sorts are inter-fertile. Thus it is clear that genes for incompatibility are present in the diploid nucleus of the young ascus and during meiosis in the ascus two sorts of nuclei arise, mutually compatible, but self-incompatible. There is, however, no segregation of sex factors as both kinds of nuclei carry the potentiality for the production of both male and female organs. In *Neurospora*, where definite sperm cells and antherids have not been discovered, the contact of the two mycelia of different sexual strain, or even of a conidium of one strain with the mycelium of the opposite strain suffices to bring about the formation of perithecia. In *Pleuraea anserina* the intermingling of the hyphae of the opposite strains is ineffective unless there is actual contact of sperm cells with trichogynes of the two strains.

Dodge and his associates (Shear, Wilcox, Aronescu) found that in *Neurospora sitophila*, which produces eight uninucleate ascospores, four represent one sexual strain and four the other. By observing the order of nuclear division in the ascus and picking out the ascospores one by one and mating up the cultures produced Lindegren determined that in about 85 percent of the cases the two strains are segregated in the first nuclear division in the ascus and in about 15 percent of the cases in the second division. In the first case the four spores at one end of the ascus are of one sexual strain and the other four of the other strain. In the second case the first two ascospores are of one strain, the next two of the opposite strain, and the last four two of one and two of the other strain. They may be arranged *aabbaabb* or *aabbbbbaa* while in the first case they will be *aaaabbbb*. Dodge also obtained fertile crosses between different species of *Neurospora*.

From all of the foregoing it seems likely that the failure to obtain perithecia in cultures grown from a single ascospore may very possibly be due in many cases to the fact that only one sexual phase is represented in the culture.

The current classifications place first in this order those families in which the perithecia stand separately upon the surface of the substratum or but slightly sunken in it. Two of these families have very thin perithecial walls. These are the FIMETARIACEAE (*Sordariaceae*) with naked or almost naked perithecia and the CHAETOMIACEAE with the perithecia covered with long hairs and with a special tuft of much longer hairs about the ostiole. The fungi in both families grow on dung or on decaying plant tissues. They are distinguished further by the fact that the asci of the former expel the ascospores through the ostiole while in the latter the asci digest and the ascospores escape in a mass of slime. It must be noted that Nannfeldt places the Chaetomiaceae in the group Plectascales as he does also the genus *Ceratostomella* (= *Ophiostoma*) mentioned above, since in both there are no paraphyses and periphyses and the asci dissolve into slime. Closely related is the FAMILY MELANOSPORACEAE, also with thin perithecial walls, often but not always with a more or less well developed neck, and with ascospores mainly inclined to be dark colored and lemon shaped as in most of the species of the two other families. *Neurospora* probably belongs here. This family because of the lighter-brown perithecia is often placed in the Order Hypocreales but seem best placed here next to the Fimetariaceae. The chief difference is the sometimes lighter colored perithecia.

The chief genera of the FIMETARIACEAE are *Fimetaria* (*Sordaria*), mostly found on dung of various animals. Some species have 4 spored asci, others asci with eight spores. The spores are surrounded by a layer of water-soluble slime on all sides except a small spot on one end. *Pleurance* (*Podospora*) is similar but the spores are two celled, one cell slender and empty, the other enlarged (Figure 63, G). There is a long gelatinous appendage at each end (sometimes several at one of the ends). *Hypocopa* is like *Fimetaria* but the perithecia are immersed in a stroma, an exceptional case for this group of families.

Chaetomium is the characteristic and most frequently found genus of the CHAETOMIACEAE. Its long ostiolar hairs may be stiff and

straight or wavy or loosely or tightly coiled, depending upon the species. The spores are mostly lemon shaped and dark colored, one celled. Various species are very numerous on damp straw, pasteboard, etc., as well as on manure.

FAMILY SPHAERIACEAE.—Perithecia with firmer wall with simple ostiole or at most with a low papilla. Stroma lacking. Perithecia superficial on the substratum or at most on a felty mass of mycelium (subiculum). Of the twenty or more genera in the family *Rosellinia* deserves mention because of the widespread occurrence of its species (over 200 are known from all parts of the world), mostly on wood and bark. Several species are dangerous parasites, e.g. *R. necatrix* on the roots and underground portions of the stems of the grape (*Vitis*). The perithecia of *Rosellinia* are nearly spherical, with a small ostiolar papilla, sitting externally on the host in a more or less well developed subiculum. The ellipsoidal, colored, one-celled ascospores are 8 in each ascus. Filamentous paraphyses are present. Because of the ascospore characters, Vincens, Wehmeyer and others suggest that this genus belongs more properly with the Xylariaceae. Other genera in the family vary as to color and number of cells in the ascospores, as well as to the hairiness of the perithecia. In many genera, at least, the asci ripen successively and project one or two at a time from the ostiole to discharge their spores, the emptied asci contracting back into the perithecium and giving place for the next maturing asci.

The CERATOSTOMATACEAE have much longer ostiolar papillae or long necks. The genus *Ceratostomella* (see note above regarding Nannfeldt's ideas of classification) has a very long neck, several times as long as the diameter of the perithecium. It shows its affinities rather to the Fimetiariaceae than to the Sphaeriaceae in its thinner perithecial wall. The ascospores are hyaline, not colored as in the Fimetiariaceae. Several species of *Ceratostomella*, e.g. *C. pini*, *C. pilifera*, etc., grow on the wood of various trees whose sap-wood takes on a blue color, the so-called "sap-stain" owing to the presence of the mycelium in the wood fibres. Hedgcock and others have shown that some species have conidia produced in slimy drops at the apex of the conidiophore branches, representing the form genus *Cephalosporium*. The dreaded "Dutch Elm Disease" is reported by Buisman to have as its perfect stage *Ceratostomella ulmi* (Figure 66, A), *Graphium ulmi* being the conidial stage. This species like

those mentioned above, has been shown to have two sexual strains which must be brought into contact before perithecia will appear. *C. paradoxa* has been shown by Dade to be similar. Its conidial stage is *Thielaviopsis paradoxa*.

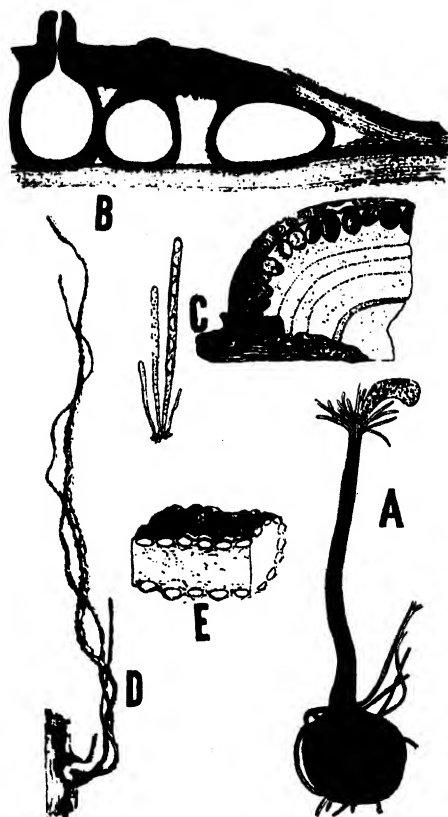


FIG. 66.—Sphaeriales. A, *Ceratostomella ulmi*; B, *Eutypella linearis*; C, *Hypoxylon marginatum*; D, *Xylaria subterranea* stroma; E, section of stroma showing imbedded perithecia. (A after Buisman, 1932; B after Vizioli, 1923; C-E after Ellis and Everhart, 1892.)

FAMILY CUCURBITARIACEAE.—Fungi with perithecia essentially superficial, as in Sphaeriaceae, but crowded upon a stroma (but not sunk in it), or if the stroma is lacking the perithecia are sunk in the substratum when young but emerge completely at maturity. In view of Julian Miller's demonstration that possibly all perithecia of this order possess a thin external stroma the reported presence or

absence of stromata in the families mentioned above and hereafter refers to a more massive structure upon or within which the perithecia are situated. Transition forms make the distinction of the two families none too easy. The ascospores are of various types as in the Sphaeriaceae. In some species conidia are formed in pycnidia. *Cucurbitaria* is the largest genus. It has dark-colored, muriform ascospores. Most of the members of this family are saprophytic on wood or bark, but probably some are parasitic. Nannfeldt places this genus in his group Ascoloculares because of the character of the asci, absence of true paraphyses and stromatic character of the "perithecium." Theissen and Sydow include it in the Order Pseudosphaeriales.

Partly sunk in the substratum but with the upper part of the perithecium free are the representatives of the two families AMPHISPHAERIACEAE and LOPHIOSTOMATACAE. Except for the partially enclosed base the former differ very little from the Sphaeriaceae and show many of the various spore forms characteristic of that family. The Lophiostomataceae are very similar except that the ostiolar papilla is compressed so that the ostiole is a slit resembling somewhat the ostiole of the Hysteriales. This resemblance is only superficial for the lateral compression is confined to the ostiole and ostiolar papilla in the one and the whole apothecium is laterally compressed in the other group. *Amphisphaeria* and *Lophiostoma* are respectively the largest genera of the two families. Most of the species of these families are saprophytic on bark, wood or dead herbaceous stems. Possibly a few species are parasitic. Conidial stages are known for only a few forms. These two families and the two next are possibly better placed with the preceding one in the Pseudosphaeriales which will be discussed later.

Next to be considered in the usual classification of the families of this order are several families whose perithecia remain entirely sunken in the substratum except for the projecting ostiole. Most of them lack a distinct stroma except occasionally a thin crust-like stroma (clypeus) connecting the upper parts of the perithecia. Many of the genera have well developed conidial stages of various types. Here are found numerous parasitic species including many that cause plant diseases of considerable economic importance. The validity of the customary family distinctions in this group of families is strongly to be doubted, particularly the distinctions

between the *Mycosphaerellaceae* and the *Pleosporaceae*. In both of these the perithecia are rather small, mostly subepidermal, with only the ostioles projecting or by the weathering away of the epidermis the whole perithecium laid bare. The perithecial walls are rather thin and delicate. The asci are not thickened much apically and in the majority of cases stretch considerably at maturity, often projecting through the ostiole before discharging their spores. The absence or presence of paraphyses, the distinction used to separate these two families seems not to hold for all species and genera. Many of the species formerly included in these families have been removed in recent years to the Order *Pseudosphaerales*. How fully this is justified and to what extent the species as yet not studied in this regard will have to be transferred must await life history studies.

In the *MYCOSPHAERELLACEAE* the genera *Guignardia* and *Mycosphaerella* deserve attention. *G. bidwellii* is the cause of the very destructive black-rot of the grape (*Vitis*). Native to North America it has been introduced into Europe where it has caused great damage to the more susceptible *V. vinifera*. The fungus attacks the leaves on which it produces brown dead spots and the fruits which become dark-colored and shrunken. In these leaf spots and shriveled berries are produced numerous pycnidia in which arise hyaline, ellipsoidal spores (*Phoma* stage of the fungus). In the leaves and berries overwintering on the ground there develop perithecia in which are produced clusters of eight-spored asci. Paraphyses are not present. Each hyaline ascospore just at maturity forms a septum dividing it into two quite unequal parts. The formation in pycnidium-like structures of "micro-conidia" which do not appear to be capable of germination leads to the suggestion that we should search here for fertilization of a trichogyne by sperm cells. *Mycosphaerella* contains over 1000 species, many of them parasites of great economic importance. The ascospores are hyaline or pale green with a nearly median septum. The conidial forms are of several types. Thus *Mycosphaerella fragariae* which causes the leaf-spot of strawberry (*Fragaria*) has as its conidial stage *Ramularia tulasnei*. The brown conidiophores project through the stomata of the diseased spots and produce terminally short chains of cylindrical or rod-shaped hyaline conidia which are produced in acropetal order. In *M. sentina* on the leaves of the pear (*Pirus*) the conidial stage was formerly known

as *Septoria pyricola*. Here the very long slender hyaline conidia are produced in pycnidia in the leaf spots. The form known as *Cercospora cerasella* is the conidial stage of *M. cerasella* on cherry leaves (*Prunus*). The brown conidiophores emerge from the stomata of the leaf spots and bear terminally, or almost so, single elongated several-celled hyaline conidia, tapering somewhat toward the apical end. When one falls off the conidiophore elongates slightly in a sympodial manner and produces another conidium, and so on until eventually an old conidiophore may show the scars of attachment of a number of conidia. *Mycosphaerella pinodes* on the pea (*Pisum*) produces pycnidia containing 2-celled hyaline conidia (*Ascochyta pisi*) while *M. tabifica* of the beet (*Beta*) has as its conidial stage *Phoma betae* in which the pycnidia contain hyaline ellipsoidal conidia. In all these species and others like them the conidial stage is the destructive stage while the perithecia are produced in the dead overwintering tissues. The different types of conidial production have been used by Klebahn as a basis for segregating the genus into several genera, e.g. *Ramularisphaerella*, *Septorisphaerella*, *Cercosphaerella*, etc.

In the FAMILY PLEOSPORACEAE the genus *Physalospora* has hyaline or pale brown ellipsoidal ascospores. In *P. cydoniae*, which forms its perithecial stage only on dead twigs, the conidial stage is the destructive *Sphaeropsis malorum*, which causes the black-rot of the fruit and the twig blight and canker of the apple (*Malus*) and quince (*Cydonia*). The conidia are produced in pycnidia and are large, ellipsoidal and dark colored. *Venturia inaequalis*, the cause of the scab of apple leaves and fruits, forms its perithecia in the overwintered leaves infected the previous summer. Its two celled, slightly colored ascospores are expelled sometimes to a height of 15 mm. The conidial stage (*Fusicladium dendriticum*) develops subcuticularly on the leaves and fruit. In this species both Killian and Frey have shown that a well-developed antherid unites with the trichogyne which terminates the coiled ascogonium and several male nuclei pass into it and by successive dissolution of the intervening septa reach the oogone cell. Subsequently ascogenous hyphae are produced. *Pleospora* has dark-colored muriform ascospores. In some species the conidia belong to the form genus *Alternaria* in which the muriform conidia are produced acropetally, so that the basal conidium is the oldest and the apical conidium the youngest.

Some species are apparently parasitic but the majority seem to be saprophytic. The foregoing genera and *Leptosphaeria*, whose colored ascospores are transversely septate into several cells, are placed by some writers in the Pseudosphaeriales (included in Nannfeldt's Ascoloculares) with perhaps not sufficient justification until the ontogeny of all the genera of this group of families has been carefully studied.

Differing from these families are the GNOMONIACEAE in which the neck of the sunken perithecium is much longer and projects well above the surface, while the asci have a thickened apex traversed at maturity by a pore. Many of the species are parasitic, but the perithecia are produced on dead host tissues. Conidial forms are known for many species. They are usually produced in acervuli, in gummy masses which are distributed by rain and insects, etc. when wet, but harden into a horny mass when dry. In *Gnomonia* the perithecia are not in a stroma. *G. veneta* of the plane tree or sycamore (*Platanus*) has conidial forms, in various stages of development, that have been described in the following form genera: *Gloeosporium*, *Discula*, *Sporonema* and *Fusicoccum*. This causes leaf scorch and leaf fall and killing of the twigs and sometimes of the larger branches. *Glomerella* is like *Gnomonia* except that the perithecia are imbedded in a stroma. *Glomerella cingulata* is found on large numbers of hosts and has for its conidial stage forms that have been described as *Colletotrichum* and *Gloeosporium* depending upon the presence or absence respectively of setae around the edge of the acervulus. This species causes various forms of diseases, viz. bitter-rot of apple (*Malus*), wither-tip of the twigs and tear stain of the fruits of orange (*Citrus*), anthracnose of mango (*Mangifera*) and avocado (*Persea*).

In contrast to the foregoing families in which in the main the perithecia are not immersed in a fungus stroma there is found a group of fungi with varying degrees of stromatic development. Lindau, in Engler and Prantl's *Die Natürlichen Pflanzenfamilien*, divides these organisms into five families: Valsaceae, Melanconidaceae, Diatrypaceae, Melogrammataceae, and Xylariaceae. The modern mycologists are inclined to reduce the first four to two families, thus recognizing only three families. The most extensive recent work on this group is the series of studies by Wehmeyer on the life histories of these fungi. He points out that these stromatic

forms exhibit a gradual transition from fungi in which the stroma is vague in outline and not very definite in structure to those with highly organized stroma. In the simplest type of stroma the surface of the substratum is blackened by the coloring of the mycelium at the surface. "The next step in stromatic development comes about by the proliferation of the mycelium within the substratum. As this formation of mycelium increases it usually becomes more or less localized about the forming perithecia" (Wehmeyer). A distinction appears between ectostroma and entostroma. "Ectostroma is that portion of the stroma which is formed on the surface of the bark, beneath or within the periderm, and which consists typically of fungous tissue only, except that when it is developed within the periderm it may contain the remnants of the periderm cells, but never of the bark cortex cells. An entostroma is that portion of the stroma which develops within the cortical or woody tissue of the host or substratum and is made up of components of both fungous and host tissues or substratum tissues." As the entostroma develops in the progressive specialization of the stroma "there is usually correlated, very often beneath a differentiated ectostroma, a clustering of the perithecia." This entostroma is often delimited from the surrounding tissues by a thin zone of blackened tissue, forming the black line visible on cutting through the host tissue. Among the variations found in this group of organisms may be noted the following: In a fruiting area (i.e. the region where the perithecia or clusters of perithecia are formed) the perithecia may be scattered or clustered, with or without an entostromatic mycelium about these perithecia. If present the "entostromatic area may or may not be surrounded by a darkened unorganized zone." It may be lighter in color than the surrounding bark tissue. The ostioles of the perithecia may be separately or collectively erumpent, even clustered perithecia not necessarily being collectively erumpent. A stroma may be *effused*, i.e. containing numerous separately erumpent perithecia or several clusters of perithecia, or *isolated*, when it contains only one cluster of perithecia. The portion of the stroma which is erumpent through the periderm or epidermis is the disk. It may be conical or cushion shaped, well distinguished from the entostroma or grading into it.

The three families of the stromatic Sphaeriales may be distinguished as follows:

FAMILY ALLANTOSPHAERIACEAE.—Stroma showing all degrees of development described above, but not entirely of fungal structure. Asci with more or less elongated tapering stalks, forming a persistent hymenial layer. Paraphyses mostly evanescent at maturity. Ascospores mostly allantoid, yellowish hyaline, sometimes inequilaterally ellipsoid and brown. Conidia long cylindrical to filiform.

FAMILY DIAPORTHACEAE.—Stroma as in the foregoing family. Asci with short evanescent stalks soluble in water so that at maturity the free asci and spores form a loose central mass. Paraphyses present. Ascospores ellipsoidal, fusoid, less commonly allantoid, or long cylindrical; hyaline or colored. Conidia of two types: short-cylindrical to filiform and ellipsoid to long cylindrical.

FAMILY XYLARIACEAE.—Stroma well developed, entirely fungal, almost always external, at least eventually, covered at first by a conidial layer. Asci long, cylindrical, ascospores 1-celled, inequilaterally ellipsoid, dark brown, paraphyses filiform.

The following genera may be mentioned briefly as they are mostly very frequent:

FAMILY ALLANTOSPHAERIACEAE.—*Diatrype*.—Stroma effuse or isolated, ectostroma deciduous, exposing a widely erumpent entostromatic disc. Perithecia parallel, separately erumpent. Ascospores 8, allantoid. Many species. Saprophytes or weak parasites on twigs and branches. *Diatrypella* is similar in many respects but the ascospores are numerous in the ascus. *Eutypella*, much as in *Diatrype* but the perithecia clustered and collectively erumpent (Figure 66, B). *Anthostoma*, stroma effuse or isolated, perithecia separately or collectively erumpent; asci, in contrast to the foregoing genera, cylindrical, short stalked, the 8 ascospores inequilaterally ellipsoid and dark brown. A transitional form in ascus and spore structure to the Xylariaceae.

FAMILY DIAPORTHACEAE.—*Diaportha*; 600 or more species. Stroma effuse or isolated. Entostroma light colored, with dark border zone. Ascospores ellipsoid or fusoid, hyaline, 2-celled. Imperfect stage belonging to the form genus *Phomopsis*. *Valsa*: Stromata isolated, perithecia clustered in the unaltered bark tissues beneath a distinct conical ectostroma. No marginal zone. Ascospores 8, allantoid, 1-celled, hyaline. Imperfect stage belonging to the form genus *Cytospora*. *Leucostoma*: Stromata isolated or confluent. Dark marginal zone about each perithecial cluster.

Asci and spores as in *Valsa*. *Valsella* as in *Leucostoma* but asci polysporous. *Endothia*: Stromata isolated or confluent. Entostroma strongly developed, colored. Ascospores 8, allantoid to ellipsoidal, 1 or 2 celled. *E. parasitica* is the fungus which has destroyed nearly all the trees of the American chestnut (*Castanea dentata*) since the fungus was introduced from Eastern Asia on nursery stock about 1900.

FAMILY XYLARIACEAE.—Because of the similarity of ascus and ascospore structure in this family and in *Anthostoma* of the Allantosphaeriaceae and of some species of *Rosellinia* in the Sphaeriaceae it has been suggested that a more natural classification would group these two genera with the Xylariaceae. Among the genera undoubtedly belonging to this family are *Hypoxylon*, stroma broadly cushion-like to almost spherical (Figure 66, C). In this genus as well as the following genera the conidial layer is external. A number of species on logs, stumps, branches, etc. *Daldinia*, stroma large, rounded, with pronounced concentric zones visible in vertical section. On dead trunks and branches. *Xylaria*, stroma upright, slender or stout, simple or branched (Figure 66, D, E). *X. polymorpha* forms thick black clubs usually growing on buried wood. These are 5 to 8 or more centimeters tall and 1 to 2 cm. thick, rounded at the apex and velvety at the base. The interior of the stroma is firm and white, the numerous perithecia forming a distinct layer just beneath the surface. The young stromata are brown and covered with a conidial layer. In *X. hypoxylon* the basal and apical portions of the slender, usually more or less forked stroma are sterile. *Daldinia concentrica* occurring on dead limbs of trees etc. may attain a diameter up to 5 cm.

Order Pyrenulales.—The perithecial lichens make up a group of about 15 families, over 80 genera and over 2000 species. They form typical lichen thalli in combination with various algal hosts. Most of the species are crustose or foliose, in only two genera fruticose. The order does not seem to form a compact monophyletic group but its various families seem rather to show relationship to various families of the Sphaeriales and perhaps to some of the Pseudosphaeriales. The perithecia may be sunk singly in the thallus (Figure 45, G) or may be produced in a stroma strongly resembling that of *Diatrype*. Among the common genera may be mentioned *Verrucaria*, with nearly 300 species forming crustose

growths on rocks into which the hyphae may penetrate a considerable distance. The perithecia are black and sunken in a thallus. The 8 ascospores are 1-celled, ellipsoidal and hyaline or brown. The host alga is *Protococcus* or *Palmella*. *Pyrenula* includes about 175 species usually on bark, growing on the alga *Trentepohlia*. The perithecia resemble those of *Verrucaria*, but the ascospores are several celled. Long slender conidia are produced in pycnidia. *Trypethelium* consists of about 75, bark-inhabiting species, mostly tropical and subtropical, whose perithecia are produced in a cushion-like stroma. The thirty-seven or more species of *Astrothelium* are also tropical or subtropical, on bark. Their perithecia are arranged radially in a stroma with their long necks approximated or joining into a common ostiole. Practically nothing is known as to the sexual reproduction of the plants assigned to this order. Spermatogonia are known in many species and may function as they are known to do elsewhere.

The old Order **Hypocreales** shows a close parallelism as to perithecial forms with the Sphaeriales. The two orders are customarily distinguished from one another by the consistency and color of the perithecia. In the latter order the perithecia are dark-colored and leathery or brittle, while in the former they are bright-colored (rarely dark) and fleshy to leathery. There are border forms such as the genus *Melanospora* which has sometimes been placed in one and sometimes in the other order but which has been treated under the Sphaeriales in this work. The genera of the Hypocreales may be placed in a series very much like that of the Sphaeriales. First come the forms with scattered superficial perithecia, then those with perithecia crowded on the surface of a stroma, those with perithecia buried in the substratum or in an internal or external stroma. A further group includes forms in which the perithecia buried in a stroma do not have well developed walls of their own but represent perithecial cavities in the stroma. Only this last type does not have its counterpart in the Sphaeriales. The ascospores, as in the latter order, vary from ellipsoidal and 1-celled to 2-celled, phragmosporous and muriform or even thread-like. Some are brown but the majority are hyaline or bright colored. Conidial fructifications are rather wide-spread in this order. The conidiophores may be separate and external or they may be packed closely together side by side or may be enclosed in a pycnidium or united into a stalked head (*Stilbum*

type). Many of the approximately 1000 species are saprophytic, others are parasitic in the leaves, stems and roots or other portions of higher plants; still others are parasitic on fungi or upon insects.

The course of sexual reproduction has been worked out completely in a few forms, but, as mentioned for the Sphaeriales, only enough is known to make certain that vastly more must be found out before the knowledge may be used to modify the current system of classification. The latter, as in the Sphaeriales, is largely based upon the characters of the mature perithecium.

In a number of Hypocreales a coiled ascogonium and antherid are known. In *Polystigma rubrum*, parasitic in the leaves of the plum (*Prunus domestica*), Blackman and Welsford and also Nienburg have shown that the ascogonium is a stout thread with several coils of mostly plurinucleate cells and tapering into a slender, sometimes branched trichogyne which may extend through a stoma but apparently more frequently does not do so. Organs exist which have been called spermagonia. Whether they really are properly so-called remains in doubt. They usually appear some time after the ascogonia do and their spores are long and slender and curved, like some of the conidia of the Diaporthaceae. No connection between one of these spores and trichogyne has been observed. Eventually, according to Nienburg, the wall breaks down between a multinucleate ascogonial cell and the large uninucleate oogone cell next to it and one nucleus passes into the oogone. Later ascogenous hyphae are sent out from the latter and eventually give rise to asci. In *Claviceps purpurea*, ergot, the germinating sclerotia give rise to stalked heads in which arise the perithecial primordia (Figure 67). This consists for each perithecium, according to Killian, of a multinucleate rounded oogone from whose base branch out one or two antherids, likewise plurinucleate. One of these antherids comes into contact with the oogone at its tip and an opening is formed through which the male nuclei enter the oogone. This gives rise, how is not known because certain stages were missing in the investigation reported, to a series of binucleate cells which develop to ascogenous hyphae forming asci by the hook method.

The sixty or more genera making up the order are variously assigned to one family, to three families or to still more. The basis of distinction is the presence or absence of stromata, the location of the perithecia, and the type of the ascospores. A number of

genera with perithecial cavities in a stroma but without well developed perithecial walls, and with long slender ascospores without paraphyses seem to constitute a natural, well defined family the CLAVICIPITACEAE. Those with ascospores not of this type and with distinct perithecia buried in a stroma are usually called the HYPOCREACEAE while those with perithecia external, with or without a stroma are placed in the NECTRIACEAE. The following genera should be noted: *Nectria*. Perithecia external to the substratum or to an external stroma on the substratum, round, with short ostiolar papilla or none, usually light colored, asci in a tuft at the base of the perithecial cavity, ascospores 2-celled, hyaline. Often parasitic on twigs or other plant tissues. In some species, e.g. *N. cinnabarina*, there first arises a cushion-like pseudoparenchymatous stroma which bears on its outer surface a dense layer of slender conidiophores, each bearing a small ellipsoidal spore (*Tubercularia* stage). Later, around the base and eventually all over the stroma arise the round, rather thick walled perithecia from whose ostioles escape eventually the hyaline, two-celled ascospores. Over 250 species are described. The presence or absence of the stroma has been used by some mycologists to distinguish two genera. *Hypomyces* with 50 or so species produces a felt-like stroma over the surface of various host species of Agaricaceae, Polyporaceae, etc. Partly sunken in the hyphae forming the stroma or entirely superficial to them occur the perithecia which, except for the stromatal character, are essentially like those of *Nectria*. *Gibberella* produces its blue or violet colored perithecia on stems, grain, etc., of various plants. Its ascospores vary from 2 to several celled. *G. saubinetii* is the cause of scab and root rot of wheat and other cereal grasses and of the root-rot of maize (*Zea mays*). Its asexual reproduction is by the abundant production of several-celled, sickle-shaped conidia. (*Fusarium* stage). Subsequently the perithecia appear. *Sphaerostilbe* has perithecia and ascospores as in *Nectria* but these arise around the base of a stalked conidial head of the *Stilbum* type. It is mostly parasitic on scale insects and other insects infesting the twigs or leaves upon which the fungus is found. *Polystigma* develops its perithecia in stromata within the host leaf. *Hypocrea* has perithecia much like those of *Nectria*, but buried in a bright-colored stroma which resembles in many ways that of *Hypoxylon* of the Xylariaceae. Over 110 species are known. In the FAMILY

CLAVICIPITACEAE may be mentioned *Epichloe* whose stroma surrounds the stems of various grasses with a thick white band in which eventually the perithecia appear; *Cordyceps*, parasitic on insects (one or two species on subterranean fungi) from which grow slender stalks bearing a head in which arise the numerous perithecia. *Claviceps*, the ergot fungus, with a dozen species or more, produces its purple sclerotia in the spikelets of grasses and related plants. On the ground, usually after overwintering, they send out stalked



FIG. 67.—Hypocreales. Perithecial stromata developing from sclerotium of *Claviceps purpurea*. (Original, F. C. Strong.)

stromatic heads in which the perithecia arise (Figure 67). The ascospores infect the flower heads of the host species where an external conidia-bearing layer is produced. These conidia are in part insect borne to other grasses. Eventually the sclerotia appear. *C. purpurea* (*Spermoedia clavus*) is the commonest species of ergot. It occurs in cultivated rye (*Secale*), less often in wheat (*Triticum*), and in many other grasses. The fresh sclerotia have considerable medicinal value. They are poisonous when eaten in large quantity as happens in time of famine when highly ergotized rye or wheat is consumed by the underfed populace.

The author has long contended that the color and consistency of the perithecium or stroma are not at all satisfactory as a basis of distinction into two orders Sphaeriales and Hypocreales. The

structure and mode of development of the perithecium are of far greater value for determining the true relationships. Many of the Hypocreales should be placed in the Sphaeriales and perhaps some in the Pseudosphaeriales.

In contrast to the undoubted Sphaeriales, i.e. those forms with true ostiolate perithecia with asci arising from the bottom and sides of the perithecial wall in a common perithecial cavity, and with periphyses near the ostiole and paraphyses among the asci are a large number of genera formerly more or less closely associated with that order. Of these the **Order Dothideales** is still recognized in most works as a distinct order. It is usually defined as consisting of fungi parasitic usually on leaves, producing endophyllous or epiphyllous stromata within which arise perithecial cavities which lack definite perithecial walls. Most of the species are tropical or subtropical, but a few forms included in the order reach the North Temperate zone, e.g. *Systemma ulmi* and *Phyllachora graminis*.

The two most important families usually placed in this order are the following:

FAMILY DOTHIDEACEAE.—Stroma arising subepidermally or subcuticularly but becoming exposed by rupture of the epidermis or growing out on slender connecting fungous masses which spread out into an external stroma. In this external stroma develop the perithecial cavities. In *Systemma ulmi* the primary subcuticular stroma produces a conidial layer. This sloughs off and the secondary stroma arises from deeper in the leaf tissues.

FAMILY PHYLLACHORACEAE.—Stroma endophyllous.—In a few cases elongated conidia may be found in subepidermal pycnidial cavities, followed by the development of the perithecial cavities in the stroma within the leaf. The stroma is frequently well organized only near the leaf surface, the mesophyllic stroma consisting of less densely compacted hyphae intermingled with remains of the host cells. In *Phyllachora graminis* this interior stroma is rather loose in its structure. There seem to be definite perithecial walls. *P. graminis* is found in the leaves of many grasses, e.g. *Bromus*, *Hystrix*, *Elymus*, etc., the elongated black stromata having the appearance of not yet opened rust sori.

In their monograph of this order Theissen and Sydow recognized four families (two of which they later removed to other orders), 140 genera and over 8000 species.

Recent studies by various authors (e.g. Petrak, Blain, Nannfeldt) have thrown grave doubt upon the validity of the Dothideales as an independent order. Orton and Petrak seem to have demonstrated that *Phyllachora* and possibly the whole family Phyllachoraceae, has true perithecia and should therefore be removed to the Sphaeriales. Other genera, usually included in the Family Dothideaceae, seem to belong with the Hemisphaeriales and still others in the Pseudosphaeriales.

The three orders Hemisphaeriales, Pseudosphaeriales and Myriangiales are stromatic forms, without true perithecia. In the first two, at least, the asci arise from ascogenous hyphae in the midst of a more or less pseudoparenchymatous stromatic tissue and gradually by pressure, aided perhaps by solution of the tissues, make cavities within which each ascus lies alone, separated from the next ascus by a thicker or thinner remnant of the original stromatic tissue. This intervening stromatic tissue, where the asci are close together, was in many cases formerly mistaken for paraphyses but can be distinguished by the fact that it is fastened above as well as below, and often laterally. Those forms in which the "paraphyses" are described as attached reticulately to each other belong in this series as do those where the tips of the "paraphyses" form a continuous pseudoparenchyma above the apices of the asci. The asci are never operculate. They are usually much thickened, at least upward, and are obovoid or clavate, rarely slender and cylindrical. The ascospores vary from one-celled and hyaline to phragmosporous and muriform, sometimes hyaline and sometimes colored. The stromata may resemble simple perithecia, the central portion of the apex breaking away as a pseudo-ostiole. The asci may arise parallel in a row at the bottom of the cavity or they may arise in a fan-shaped cluster from a raised "placenta" at the center of the base. In the latter type there are usually no paraphysis-like remnants of the stromatic tissue, this having been dissolved or pushed back as the asci grew, while in the former type these fragments usually persist long. Petrak, Gäumann and others are inclined to consider all perithecium-like structures with a spreading, non-paraphysate basal cluster of asci as Pseudosphaeriaceous, even though the spore-fruit may appear to possess a true perithecial wall and a typically developed ostiole lined with periphyses. Whether such forms are in reality intermediate, as they believe, between the

Pseudosphaeriales and the Sphaeriales or not will require much further investigation to determine. It seems clear that the typical Pseudosphaeriaceous structure is very different from the true Sphaeriaceous structure. Perhaps Nannfeldt is right in questioning the validity of the assumption of such intermediate forms, drawing the distinction not so much on the external and structural characters of the wall as on the nature of the hymenium. If true paraphyses (the metaphyses of Petrak) arise from the floor of the perithecium among the slender mostly parallel asci, ending free above, these are to be considered as true Sphaeriales, while the fan-like spreading, broader asci which entirely crowd back the stromatic tissues, or the rather broad, thick-walled asci which arise in monascous cavities, leaving paraphysis-like threads attached both above and below, indicate their connection to the Pseudosphaeriales, even if the external structures are similar. Unless the latter position is taken we have the anomaly of one genus, *Leptosphaeria*, with some species considered as Pseudosphaeriales, others as intermediate forms, and still others as true Sphaeriales (Petrak, Gäumann). The forms with more massive stromata may have at maturity several cavities of the typical Pseudosphaeriaceous type or with these perithecial cavities formed in projections from the main stroma. These would represent forms formerly placed respectively in the Dothideales and in the Family Cucurbitariaceae of the Sphaeriales. Where the stromata have been developed superficially on the leaves of the host they are mostly small, hemispherical or disk-like, with the upper surface firmer and the lower portion less firmly developed. They open at the top by a more or less ragged tearing of the tissue. In the interior there may be separate monascous cavities or the central tissues may be dissolved as in some of the Pseudosphaeriales leaving a cavity with a cluster of paraphysate asci. Such fungi form the **Order Hemisphaeriales**, perhaps the majority of which were formerly included in the older Order Perisporiales. von Höhnelt considers some of the Microthyriaceae to be related to *Meliola* in this latter order.

The more massive stromatic structures of the Myriangiales do not show such similarities to the Sphaeriales as either of the foregoing orders. The asci are thick-walled and spherical and are produced in monascous locules, sometimes scattered apparently without order

in the tissues of the stroma. The ascospores are eight in number, phragmosporous or muriform, and usually colored.

Order Hemisphaeriales.—The older interpretation of the fruiting bodies was a perithecium with the basal portion poorly developed while a more or less shield shaped perithecial wall formed the upper half. It is now interpreted as a stroma with a hyphal or pseudoparenchymatous basal portion and a firmer upper part. At the apex by breaking of the tissues a pseudo-ostiole is formed. Another view which once received strong support on the part of a number of mycologists was to consider this structure as a small apothecium with poorly developed hypothecium and with a more or less permanent and rather late-opening cover, as in the Phacidiales, to which this order was by this theory believed to be related. von Höhnelt believes that certain Microthyriaceae are forms transitional to the Discomyceteae. The order consists of fungi which are entirely superficial or subcuticular or which have a hypodermal stroma connected with the epiphyllous stroma by strands of hyphae emerging through the stomata or other openings. Asexual reproduction is known in a few forms and consists of the formation of conidia from some of the external hyphae or in pycnidial structures. With few exceptions the 111 or more genera and over 300 species are leaf parasites, largely tropical but represented in the temperate zones by a number of genera. Arnaud has studied the structures of many of these fungi, especially in relation to the host tissues.

Killian has studied the sexual reproduction in *Stigmatea robertiani*, a form previously included in Family Mycosphaerellaceae of the Sphaeriales, and the validity of whose transfer to this order is not at all sure. There develops a subcuticular pseudoparenchymatous layer, within the thicker central portion of which appear several short cells one of which becomes a binucleate oogone with a receptive papilla and another a binucleate antherid. After the fusion of these cells there follow several nuclear divisions and a fusion of male and female nuclei. The resultant diploid nuclei pass out into the ascogenous hyphae which give rise to asci arising from the floor of the perithecium in between the loose stromatic hyphae. This hypothecial floor is pseudoparenchymatous and the top is hemispherical, of radially arranged hyphae which break to leave a central ostiole. Several functional oogones and antherids may be found for each stroma as in the formation of the apothecium in *Pyronema*.

Theissen and Sydow recognize five families in this order, as follows:

FAMILY STIGMATEACEAE.—Upper surface of radially arranged hyphae, arising subcuticularly, vegetative mycelium lacking or almost so. Eleven genera of which *Stigmatea* is the type genus of the family.

FAMILY POLYSTOMELLACEAE.—Stromata with radial structure as in preceding, but external to the cuticle and arising from an internal mycelium ("hypostroma") from which emerge strands through the epidermis at various points to give rise to the stromata. 39 genera of which 20 form very narrow perithecia, formerly being placed in the Hysteriales. *Parmularia* (perhaps more correctly named *Schnecpia*) belongs here. It was mentioned among the Hysteriales. *Polystomella* is the type genus of the family.

FAMILY MICROTHYRIACEAE.—Stromata with radial structure, vegetative mycelium and stromata entirely superficial. 36 genera with over 150 species, all but a few leaf parasites. Here and there on the more or less reticulately arranged coarse brown vegetative mycelium (which is lacking in a few genera) appear the almost lens-shaped stromata. In each, under the radial, centrally ostiolate cover, is a hymenium of vertically standing asci intermingled with conspicuous or inconspicuous (rarely lacking) paraphysis-like remnants of the stromatic tissues, which in a few cases form a definite epithecium. The stromata are mostly round but are in some cases laterally compressed. Among the forms without vegetative mycelium is the genus *Microthyrium* in which the stromata appear as little black superficial dots on the leaves or stems of various plants. *Asterina* (Figure 68) forms small round stromata and *Lembosia* linear stromata in the brown vegetative mycelium on the surface of the host.

FAMILY TRICHOPELTACEAE.—The conspicuous mycelium is radial in arrangement, or forms sterile parallel hyphae. The cover of the stroma appears to be merely a local thickening of the vegetative mycelium. Paraphysis-like threads are lacking. Six genera are known, and from 10 to 15 or more species, all tropical.

FAMILY HEMISPHAERIACEAE.—Mycelium lacking or reticulate, superficial. Cover of the stroma not radial in structure. Under the cover there may be a single hymenium with or without paraphysis-like threads or several smaller hymenia under one cover, in some cases these being reduced to a considerable number of "monascous hymenia," i.e. imbedded in the hypothecium are scat-

tered single asci. 19 genera of mostly tropical fungi. *Micropeltis* occurs in the Old and New World tropics on leaves. Its stroma contains a single hymenium with many asci and with paraphysis-like structures and hyaline 4 to more celled ascospores.

Order Pseudosphaeriales.—The fungi included in this order have been segregated from the Sphaeriales and Perisporiales mainly,

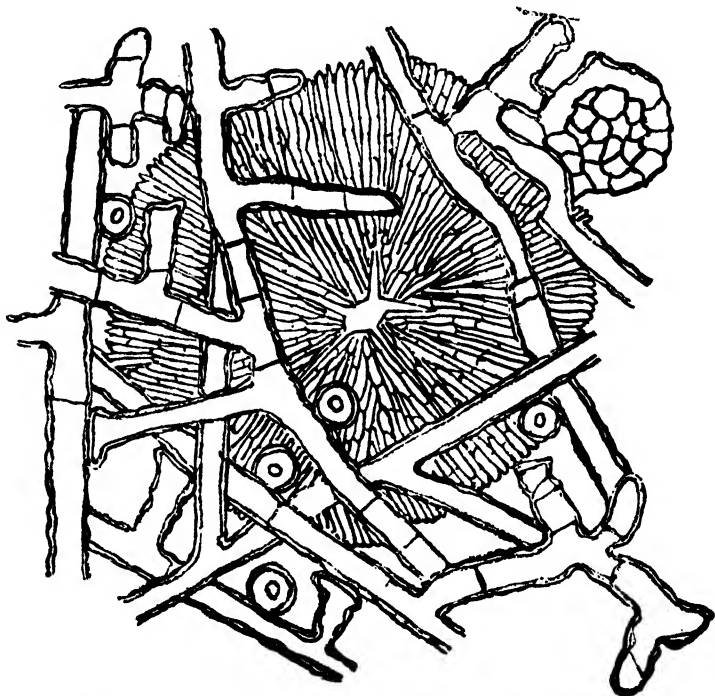


FIG. 68.—Hemisphaeriales. *Asterina camelliae*. (After Theissen and Sydow, 1917.)

and even from the Pezizales. Their true relationship is not certain, indeed it is doubtful whether the genera assigned to this order are all related. They are largely tropical, but many occur in temperate regions. They may be saprophytic or parasitic on plants or even on insects. The fruiting bodies resemble superficially perithecia or stromata of the Sphaeriales or some Dothideales. They are almost exclusively external or become external by rupture of the host tissues. They are distinguished from all the preceding orders (except a few species of the Hemisphaeriaceae with "monascous hymenia") by

the mode of occurrence of the asci. These arise in separate stromatic cavities, one ascus to each cavity. In the majority of genera they are nearly spherical and mostly 8 spored. They appear to develop somewhat as follows: Within a pseudoparenchymatous stromatic structure arise branching ascogenous hyphae, probably in many cases if not in all from an ascogonium. These hyphae grow out into the stromatic tissue, dissolving it so that eventually each terminal ascus lies in a cavity of the original sterile tissue. These asci may be separated rather widely or the separating tissue may be but a thin sheet of cells. The developing asci may arise in a fan-shaped cluster destroying the stromatic tissue as they enlarge. The ascospores vary from hyaline to brown, and from 1-celled to many celled, in many genera being muriform. The fact that the many celled type of ascospore is the most typical for the order, the 1 celled hyaline spore being found only in two genera of the supposed transitional family (Dothioraceae), casts doubt upon the idea that the Pseudosphaeriales are a somewhat primitive order from which have arisen the Sphaeriales. The asci become exposed by the weathering away of the outer part of the stroma or of the apical portion. Rarely the central apical tissues dissolve away to form an ostiole. In the forms with a small perithecium-like stroma the tissues between the ascus locules break or dissolve away leaving shreds that have been taken for paraphyses, so that the numerous asci appear to stand in a true perithecial cavity. Careful investigation has shown that many species formerly assigned to the genera *Pleospora* and *Leptosphaeria* (Family Pleosporaceae, Order Sphaeriales) have the foregoing structure, hence must be transferred to this order. Just how far this may apply to the many remaining species of these and other genera can be determined only by careful study of the development of the young perithecia. To say, as does Gäumann, that these represent a transition from one order to the other may represent the truth but the author prefers to suspend judgment until further light is thrown on the subject by ontogenetic investigations throughout the various genera of the Sphaeriales. It is possible that these are transitional forms but that evolution has progressed in the contrary direction, from the Sphaeriales to the Pseudosphaeriales. Sexual reproduction has not been investigated in enough undoubted members of the order to enable the information gained to be used in classification. Conidia are produced in a number of families.

Theissen and Sydow recognize several families. In addition to the Dothioraceae, mentioned above as a supposed transitional group the most important are the

FAMILY PSEUDOSPHAERIACEAE.—The stromata resemble separate perithecia of the Sphaeriales and open at the apex either by crum-

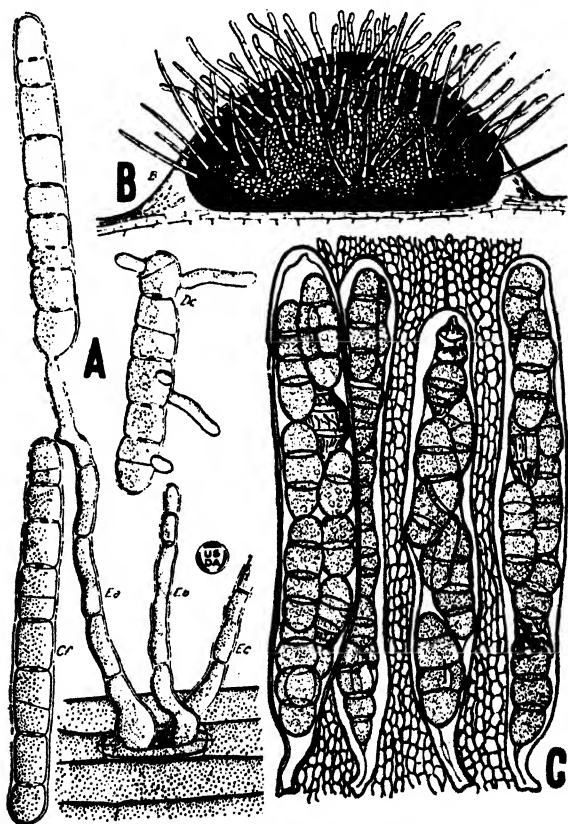


FIG. 69.—Pseudosphaeriales. *Pyrenophora teres*. A, conidiophores and conidia; B, perithecium; C, portion of interior showing asci surrounded by stromatic tissue. (After Drechsler, in Jour. Agr. Res., 1923.)

bling of the tissues or by the dissolving of the tissues to produce a true ostiole. The asci are clustered at the base, separated by paraphysis-like hyphae attached at the top as well as bottom. The interior tissues and part or all of the interlocular (paraphysis-like) walls dissolve leaving a cluster of asci at the base of a hollow

perithecium-like structure so that with mature ascocarps it can not be determined easily whether the fungus belongs to the Pseudo-sphaeriales or to the Sphaeriales. Among the fungi assigned here with more or less uncertainty are some species of *Pyrenophora*, of which *P. teres* (*P. trichostoma*) is the perfect stage of *Helminthosporium teres* (Figure 69) the cause of Net Blotch of barley, various species of *Pleospora* and *Leptosphaeria*, and *Didymella*, all formerly assigned to the Family Pleosporaceae, of the Order Sphaeriales.

Order Myriangiales.—The fungi composing this order are mainly parasitic upon insects or plants. To a large extent they are tropical and subtropical, although *Myriangium duriaei* (Figure 70, A–C) occurs in the southern part of the United States and *Elsinoe veneta* (Figure 70, D–E) is found wherever the raspberry and related fruits of the genus *Rubus* are grown in North America. It is also known in Italy. *E. pyri* is known from the Caucasus and from Switzerland. The fruiting structures are stromata, superficial or erumpent from the tissues of the host and composed largely of pseudoparenchyma. Superficially the stroma is usually dark, often lighter colored internally. Scattered apparently at random or in a more or less definite layer throughout the whole stroma or definite portions of it are monascous loculi, each separated from its neighbors by a considerable mass of not greatly altered fungous tissue. The single ascus is nearly spherical (Figure 70, B) and is thick-walled. The asci become exposed by the weathering away of the overlying tissues and then, in the presence of moisture, absorb water, swell and burst (Figure 70, C), thus setting free the eight muriform or phragmosporous spores. Asexual reproductive stages are known in a few cases. Thus the fungus formerly known as *Gloeosporium venetum* (Figure 70, E) represents the asexual stage of the fungus causing the anthracnose disease of the canes, leaves and other portions of *Rubus*, the ascigerous stage of which, *Elsinoe veneta* (Figure 70, D), is formed according to Burkholder, only on the canes in the autumn, the ascospores maturing the following spring. This perfect stage was first described by Burkholder as *Plectodiscella veneta*, but Miss Jenkins has shown that this genus is a synonym of the earlier describe *Elsinoe* of which *E. canavaliae* is a serious pest of *Canavalia* in the East Indies and *E. phaseoli* of the Lima bean (*Phaseolus lunatus*) in the West Indies. Both species attack particularly the pods on which they cause a "scab." Miss Jenkins and Shear have shown

that the conidial stages of these species should not be considered to belong to *Gloeosporium* but to the form genus *Sphaceloma*. *Myriangium duriaei* forms its black sclerotia (Figure 70, A) on the twigs of various trees where the fungus is parasitic upon various insect pests. The basal part of the stroma is more or less cushion-like. Out of the upper part grow one or more masses of somewhat lighter colored tissue in which the asci are scattered one to a locule. The asci are round, with 8 muriform spores. By the weathering away of the tissues the asci are gradually exposed. In another species, *M.*

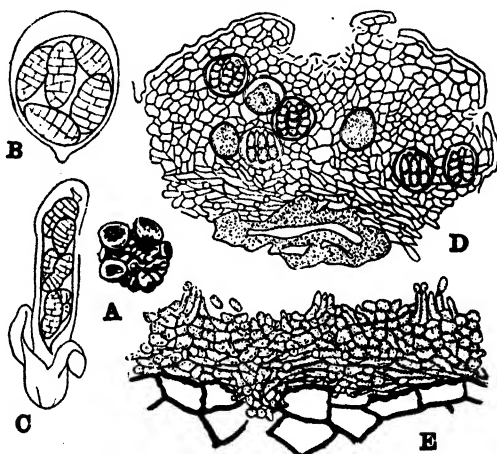


FIG. 70.—Myriangiales. A–C, *Myriangium duriaei*. A, stroma in top view; B, ascus; C, dehiscing ascus, the outer wall ruptured but the inner wall elongated but intact; D–E, *Elsinoe veneta*. D, vertical section of ascocarpic stroma; E, acervulus (*Gloeosporium venetum*) stage. (A–C after Petch, 1924; D–E after Burkholder, 1917.)

bambusae, Tai reports that the ascus has two walls, the outer being thick. At maturity this breaks at the apex and contracts downwards while the inner wall elongates, so that the outer wall forms a sort of cup-like base. The ascus ruptures at the apex, discharging the spores. A number of other genera have been described in this order, differing largely in the form and mode of attachment of the stroma and the distribution of the monascous locules.

It is to be regretted that very little is known of the earlier stages of development of the asci, in particular as to the presence or absence of sexual organs, etc. Julian Miller reports that in *Myriangium duriaei* multicellular archicarps of multinuclear cells occur in folds on the surface of the stroma. From these there grow numer-

ous ascogenous hyphae of dicaryon cells whose nuclei divide conjugately. This mass of outwardly and upwardly growing ascogenous hyphae represents the whole of the fertile upper part of the spore-fruit, there being no sterile hyphae present. From the ascogenous hyphae there bud off laterally at various levels the cells which become the asci. These then lie more or less isolated but separated, not by true stromatic tissue but by a tissue made up of tangled ascogenous hyphae. This is entirely different from what is reported for the Pseudosphaeriales in which the ascogenous hyphae grow up into a mass of stromatic tissue, dissolving out the monascous cavities in which the asci lie. If Miller's findings can be confirmed for other genera of the Myriangiales it will necessitate placing this order perhaps close to the Aspergillales and entirely outside of the groups formerly included in the "Pyrenomycetes."

Gäumann, Nannfeldt and other mycologists suggest that from such forms as the Myriangiales by crowding together and elongation of the asci and reduction of the stroma have arisen the Hemisphaeriales and Pseudosphaeriales. Gäumann and also Petrak derive the Sphaeriales directly from the latter. The fact that the ascospores of the Myriangiales are many-celled seems to the author to exclude them from the direct line of ancestry of these other orders. It appears to the author that the Sphaeriales (including closely related Hypocreales) with simple ellipsoidal hyaline or light colored spores are perhaps the more primitive and that from these by gradual loss of the distinction between perithecial wall and stroma these stromatic orders may have been derived.

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CHAPTER IX

CLASS ASCOMYCETEA: ERYSIPTHALES, ASPERGILLALES, SACCHAROMYCETALES AND ALLIED FORMS

As is the case in several other orders of the Class Ascomyceteae the investigations of the last two decades have thrown grave doubts upon the validity of some of the orders included in this chapter. This is particularly true of the **Order Erysiphales** (Perisporiales of most authors*) which certainly can not be maintained as recognized by Lindau in Engler and Prantl. For the present we must conceive of it as a group, some of whose forms are doubtless properly set apart from other orders but with so many forms that are transitional to other orders that as yet we do not know where to establish the ordinal limits. They carry on a parasitic, less often saprophytic, existence on the surface of the host plant, the parasites not even penetrating the epidermis cells in some cases (*Meliola*) or merely sending haustoria into their cells, in a few cases living in the intercellular spaces of the leaf but fruiting on the exterior. In only a few cases the perithecia develop under the cuticle or epidermis but become exposed on the rupture of the overlying layer. The mycelium is septate and to a large extent the cells are uninucleate. Asexual reproduction may be lacking or may consist of the successive formation of single conidia or of the production of a chain of conidia, the oldest conidium being the terminal one. In the Capnodiaceae and Meliolaceae (Perisporiaceae) conidia are produced sometimes in pycnidia. The perithecia arise upon the external mycelium or are partially surrounded by it (except the subcuticular or subepidermal perithecia noted above). They lack an ostiole in the Erysiphaceae and may be provided with an ostiole or lack it in the other families, and sometimes in different species of the same genus (e.g. *Capnodium*, some of whose species are ostiolate and

* In view of the fact that the type species of the genus *Perisporium*, *P. graminum*, does not belong to this order it is necessary to use an ordinal name based upon a genus recognized by all, hence the author follows the usage of Gwynne-Vaughan and adopts the name Erysiphales, based upon the genus *Erysiphe*.

others exostiolate). The perithecia may be entirely free or surrounded by the loose vegetative mycelium or, as in *Meliola*, developed beneath a sort of stromatic covering through which the apex of the perithecium later makes its way (Figure 75, A, B).

The order as recognized by Lindau, in *Die Natürlichen Pflanzenfamilien*, included three families: Erysiphaceae, Perisporiaceae and Microthyriaceae. The latter are now placed in the Order Hemisphaerales while many genera of the Perisporiaceae have been transferred to other orders. The author follows Theissen and Sydow in their classification and delimitation of this order, recognizing that further developmental studies will probably necessitate great changes. Arnaud distributes all of the families and genera formerly assigned to this order (in Lindau's sense) among various other orders. The Erysiphaceae he places in the Hypocreales, *Meliola* he places in the Dothideales, *Capnodium* in the Sphaerales, and still other forms he transfers to the Aspergillales.

Theissen and Sydow recognize four families: Erysiphaceae, Perisporiaceae, Englerulaceae and Capnodiaceae. These four will be recognized here giving the name Meliolaceae to the family formerly called Perisporiaceae for the reason that *Perisporium* does not belong to this family or even to this order.

FAMILY ERYSIPTHACEAE, the Powdery Mildews.—These fungi are parasitic upon Flowering Plants (Anthophyta) the world over, reaching their greatest development in the temperate zones. They are usually confined to leaves and young tissues of other portions of the plant, such as the young shoots, buds, fruits, etc. *Sphaerotheca phytophila* is found only on the lobed galls produced on the hackberry (*Celtis occidentalis*) by a species of mite, *Uncinula necator* attacks not only the leaves and young green shoots but also the immature berries of the grape (*Vitis*) while *Sphaerotheca mors-uvae* on the gooseberry (*Grossularia*) is confined almost exclusively to the berries. Except for the genus *Leveillula* the mycelium is superficial, obtaining its nourishment by haustoria penetrating the epidermal cells (Figure 71, A) or even to the cell layer immediately underneath or in *Phyllactinia* (Figure 71, B, C) entering the stomata and penetrating the mesophyll cells bordering the substomatal chambers. *Leveillula* (Figure 71, D) enters the leaf through the stomatal openings and is confined to the mesophyll except that the conidiophores emerge through the stomata. The

cells are always uninucleate. The conidia arise basigenously at the apex of short or elongated conidiophores. In *Leveillula* and *Phyllactinia* (Figure 72) the conidium falls off before the next succeeding conidium is formed, but in the remaining genera of the family the conidia remain attached so that a chain of conidia is produced which in *Erysiphe graminis* may consist of 20 or even more

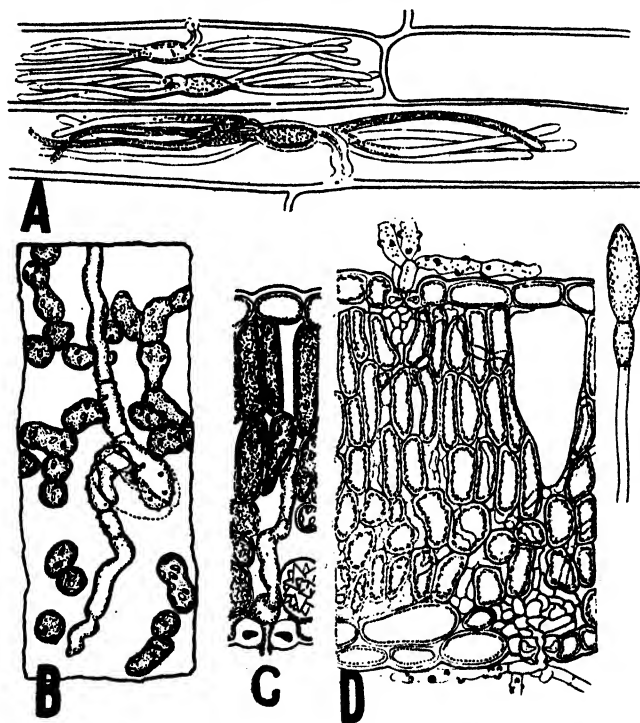


FIG. 71.—Erysiphales, Erysiphaceae. A, haustoria of *Erysiphe graminis* in epidermal cells of host, seen from above; B and C, internal mycelium of *Phyllactinia corylea*; D, external and internal mycelium of *Leveillula taurica* and conidiophore. (After Arnaud, 1921.)

before the older ones break off. Berlese reports for *Erysiphe graminis* that after a cell is cut off at the top of the conidiophore it divides into two conidia, the next cell cut off from the conidiophore dividing similarly into two conidia. Thus the terminal two conidia are of equal age and are the oldest pair, followed by younger and younger pairs toward the base of the conidial chains. The conidia are distributed by the wind and germinate in dew or rain drops

on the epidermis of the hosts, producing a short hypha which sends a haustorium into an epidermal cell. Thereafter the mycelium grows rapidly, branching in all directions, but gradually spreading radially from the point of infection. Conidial production continues for some time but eventually gives way to the production of perithecia. In some species of powdery mildews conidia only are produced on some hosts, conidia and, later, perithecia developing

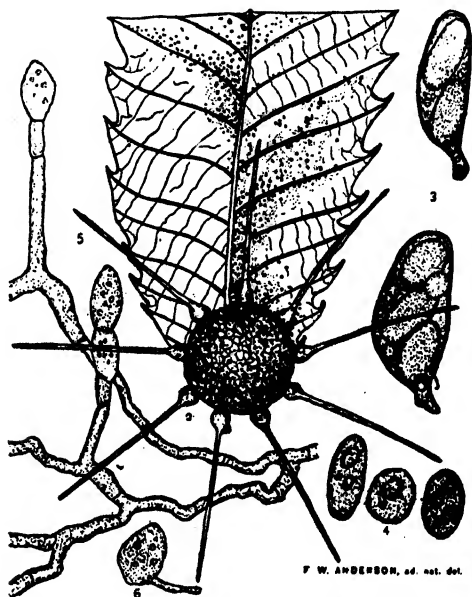


FIG. 72.—Erysiphales. *Phyllactinia corylea*. (After Ellis and Everhart, 1892.)

on other hosts. This appears to be especially true in the tropics. When perithecial development occurs it is usually on only one side of the leaf although conidia may be produced on both sides. This is not universally true.

We owe our first clear knowledge of the sexual processes in this family to Harper, in 1895 and later, although de Bary and others twenty to thirty years earlier had described the external features of the process. From neighboring hyphae in contact there arise an antheridial and an oogonial branch, each at first uninucleate (Figure 73). The latter is somewhat rounder and the former a little more slender. They become appressed side by side or may

even coil about each other a little. The antheridial branch divides into a uninucleate stipe and an apical uninucleate antherid which presses closely against the upper portion of the oogone. The oogonial branch remains unicellular or may divide into a smaller basal and larger terminal cell (the oogone proper) or the nucleus only may divide, producing a binucleate oogone one of whose nuclei eventually disintegrates. An opening is formed from the antherid into the oogone and through this the single male nucleus passes,

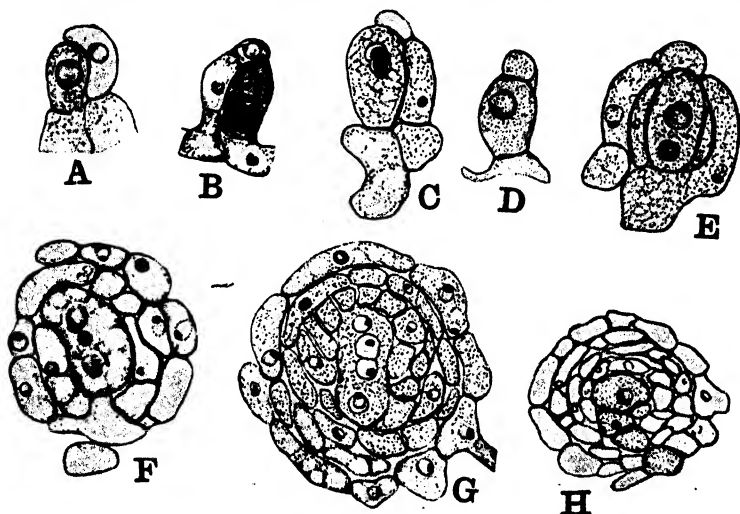


FIG. 73.—Erysiphales. Sexual reproduction of *Sphaerotheca castagnei*. A and B, development of antherid and oogone; C, fertilization of oogone, nuclei beginning to unite; D, nuclei united; E, beginning of investment by upgrowing hyphae, zygote nuclei divided; F, investing hyphae further developed, G, perithecial wall three layers thick, zygote nuclei divided into four; H, ascogenous hypha divided into four cells of which the largest will become the ascus. (After Hein, 1927.)

or the antherid nucleus divides and one nucleus passes into the oogone, the other remaining in the antherid. According to Harper and several other observers the male and female nuclei fuse (Figure 73, C, D), but according to Dangeard and his students there is no passage of a male nucleus into the oogone, hence no nuclear fusion at this stage. To the author the weight of the evidence favors Harper's view, though it is not at all unlikely that some species of this family may be apogamous, as is known to be the case in many of the Pezizales. In the mean time from the cell basal to the oogone there grow out branching hyphae which push upward and around

the oogone, with the attached antherid, and enclose them in a tangled ball of hyphae which enlarges to become the perithecium. Additional layers of hyphae arise in similar manner until the perithecial wall is usually three layers in thickness. The inner layer consists of thin-walled cells, called by Hein "nurse cells," richly filled with food while the two outer layers form the cortex. This eventually becomes dark and the outer cells become more or less polygonal in outline. The nucleus of the oogone divides rapidly and the oogone elongates, becoming an elongated plurinucleate structure which is soon divided by septa into a row of from five to eight cells, all uninucleate except the penultimate cell which remains binucleate. In *Sphaerotheca* and *Podosphaera* the two nuclei unite and this penultimate cell enlarges and becomes the single ascus. The fusion nucleus divides successively until 8 nuclei are formed. Around each nucleus part of the cytoplasm of the ascus is cut out by the formation of spore walls, thus producing the 8 ascospores, or, by degeneration of some of the nuclei or partly formed spores, a smaller number (Figure 72). The ascospores are hyaline and broadly ellipsoid. The ascus is obovoid. Harper's accounts indicate two chromosome reductions during these nuclear divisions, as would be necessary if there were nuclear fusions both in the oogone and in the ascus. Dangeard, on the contrary, who denies the occurrence of a nuclear fusion in the oogone, admits but one reduction division in the ascus. In the other genera of the family the binucleate penultimate cell of the row arising from the fertilized oogone undergoes further division and produces a number of short ascogenous hyphae made up of dicaryon cells. The terminal cell of each ascogenous hypha enlarges and the nuclei fuse and undergo division, thus giving rise to an ascus with ascospores. The latter arise as do those of *Sphaerotheca*. The number of asci may vary from five to eight (Figure 74, C) in some species up to 20 to 30 in other species. As the asci enlarge the layer of nurse cells is gradually destroyed, leaving only the usually two layered cortex. From the outer cells of the cortex arise the characteristic appendages, simple and hypha like (although sometimes colored near the base) in *Erysiphe*, *Leveillula* and *Sphaerotheca*, hooked or spirally coiled at the tip in *Uncinula*, straight and once or more dichotomously forked at the apex in *Microsphaera* and *Podosphaera*, or stiff and needle like, with a bulb like base, in *Phyllactinia* (Figure 72). In

some species the appendages are colorless, but often they are colored in their basal parts. The appendages do not seem to have the same function in all cases. They may hold the perithecia fast to the mycelium (hypha type, as in *Erysiphe*) or may curve downward and pry the perithecium loose as in some species of *Uncinula* and in *Phyllactinia*. The hooked or forked appendages would seem fitted for distribution by insects, but that has not yet been demonstrated to be the normal means of distribution. When the ascospores are mature, which may not be until the following spring, the asci absorb water and swell until the perithecium is ruptured, at which time the asci also begin to burst, discharging the enclosed ascospores with considerable force.

Homma sowed a single conidium of *Sphaerotheca fuliginea* upon its host plant and upon the resultant mycelium were produced conidia and sexual organs. He therefore considers this species to be homothallic.

Salmon in his very excellent monograph of this genus recognized but 49 species and 11 subspecies in the whole world. His species limitation is much more conservative than that of most mycologists so that it is perhaps safe to say there are from 100 to 150 species. Blumer recognizes 80 species in Central Europe alone and mentions fifty extra-limital species.

Salmon in England and Reed in the United States showed that some species are made up of biological races which are confined to but a single host species or very closely related host species. This is true of *Erysiphe graminis*, confined to grasses (Poaceae) but in which the biological race on *Poa* will not infect *Bromus* or *Triticum* and the strains on either of those genera will not affect the other. Even for the genus *Bromus* there are some races of the fungus that will attack certain host species while other species are subject to attack by other races. On the contrary *Erysiphe cichoracearum* is very widespread in its host range and conidia from the fungus on one host may infect many different hosts in families far apart systematically.

FAMILY MELIOLACEAE (*Perisporiaceae* of most authors: see footnote on page 218).—In this family, too, the mycelium is mostly superficial and spreads in a network from the initial point of infection by conidium or ascospore. The hyphae, in contrast to those of the Erysiphaceae, are usually dark in color. They may form a

dense crust or be more or less separate. They may send haustoria into the epidermal cells or even into the next layer of cells beneath or may, without producing haustoria, adhere closely to the epidermis whose outer wall becomes more or less corroded with evidence of some injury to the contents of the cell. In the genus *Pampolysporium* the mycelium and perithecia are subepidermal, in *Alina*

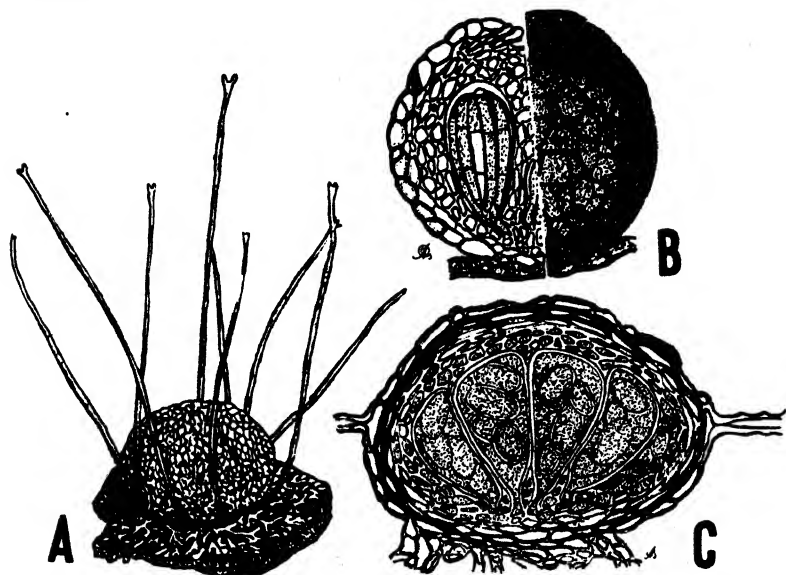


FIG. 74.—Erysiphales, A-B Meliolaceae. A, *Meliola bidentata*, perithecium; B, *Perisporina manaosensis*; C, Erysiphaceae, *Microsphaera quercina*. (A after Ellis and Everhart, 1892; B after Arnaud, 1923; C after Arnaud, 1921.)

and *Lasiobotrys* subcuticular. In *Stomatogene* and *Piline* the mycelium forms a sort of foot which penetrates through the stoma into the substomatal chamber. Conidia produced singly on the superficial mycelium are known in 1 or 2 genera; in several genera are produced ostiolate pycnidia containing numerous conidia. The perithecia are typically without appendages, mostly black or dark brown, without ostioles in the majority of genera. The asci arise in a single layer or tuft in the base of the perithecial cavity. The ascospores are usually 8 in number. They are 1-celled and hyaline in one genus but in most cases are 2 to many celled (Figure 74, B) or even muriform and either hyaline or brown. In general the ascospores do not represent types that would seem to be primitive.

The process of sexual reproduction has been worked out carefully in *Meliola circinans* by Graff. Close to one another on nearby hyphae there arise an ovoid uninucleate oogone with short stalk cell and a slender somewhat spirally wound uninucleate antherid, also with a short stalk. The two become appressed near their tips and an opening is produced. The antherid nucleus disappears and what appears to be a fusion nucleus is visible in the oogone, and what appears to be a fusion nucleus is visible in the oogone,

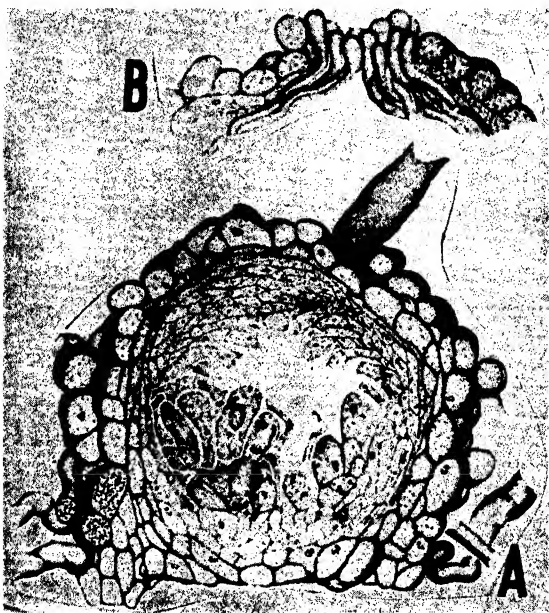


FIG. 75.—Erysiphales. *Meliola circinans*. A, Section through nearly full-grown perithecium, showing firm stromatic hood and the more delicate-walled perithecium; B, periphyses pushing through stromatic hood to form ostiole. (After Graff, 1932.)

although the passage of the male nucleus into the oogone and its fusion with the female nucleus was not observed. Over the united antherid and oogone the surrounding vegetative hyphae grow to produce a dark colored shield-like stroma (Figure 75, A, B). From the stalk cells of the oogone and antherid there grow out hyphae which form a perithecium around these organs, under the stromatic shield. The fertilized oogone elongates and divides into a number of uninucleate cells of which two or three near the apex send out

several branched ascogenous hyphae which produce typical hooks which give rise to the asci. A few paraphyses appear among the asci while from the upper part of the perithecium arise paraphyses which grow up together and penetrate the stromatic shield and spread apart to produce the ostiole (Figure 75, B). The eight nuclei produced in each ascus in the usual manner are taken up by two's in the four developing ascospores. Two of these binucleate ascospores are destroyed by the growth of the other two which eventually become 5-celled, with one nucleus in each cell except the middle cell which is binucleate. The presence of a true ostiole lined by paraphyses and the occurrence of paraphyses would seem to suggest that perhaps this genus belongs rather to the Sphaeriales.

In this family Theissen and Sydow distinguish 19 genera of which *Meliola* (Figure 74, A) and *Irene* with many hundred species are very abundant in the tropics. Stevens has attempted a monograph of the genus *Meliola* which is indispensable for the recognition of the species of this difficult genus.

FAMILY ENGLERULACEAE.—These are tropical leaf parasites whose perithecial cells dissolve into slime at maturity exposing the enclosed asci. 13 to 15 genera and 20 to 30 species.

FAMILY CAPNODIACEAE.—These are transferred by Arnaud to the Sphaeriales but it seems best to follow Theissen and Sydow in retaining them in the Erysiphales. The dark colored mycelium is usually superficial and in many cases saprophytic on "honey-dew," the sugary deposits forming on plant parts from the droppings of aphids, scale-insects, etc. This mycelium sometimes forms a black papery layer that can be peeled off from the underlying leaf. The conidia are borne in pycnidia of various shapes (Figure 76), sometimes elongated like a long-necked bottle. The external perithecial walls are formed of parallel, laterally adhering hyphae, not of polygonal cells as in the Erysiphaceae and Meliolaceae. In the same genus may be found species with ostiolate perithecia and other species with perithecia without ostioles. The perithecia may be sessile or more or less stalked, sometimes elongated like the pycnidia. The ascospores vary from colorless to colored and from 2 to many-celled. Theissen and Sydow recognize 25 or more genera and 50 or 60 species, mostly tropical or subtropical, but some found in temperate regions. *Capnodium salicinum* (Figure 76) occurs upon willow (*Salix*) leaves and twigs in Europe. *C. citri* causes "sooty mold" on oranges, etc.

(*Citrus*) wherever they are cultivated. A few species of *Limacinia* occur on leaves of trees and shrubs in temperate regions, even as far north as Germany and England.

FAMILY TRICOTHYRIACEAE.—This family of five or more genera and 20 or so species has been tossed about by mycologists since its members were first studied. Mostly these forms have been assigned to the Erysiphales or to the Hemisphaeriales, close to the Micro-



FIG. 76.—Erysiphales, Capnodiaceae. *Capnodium salicinum*, perithecium with emerging asci and pycnidium with emerging conidia, also unopened perithecium. (After Tulasne, 1863.)

thyriaceae. They are tropical, parasitic on the epiphyllous mycelium of *Meliola* and other fungi. The perithecia are more or less round and by the curving back of their supporting hyphae come to lie with the base outermost. Thus the tuft of asci spreads outward and downward from the apparent top side (ontogenetically the base) of the perithecium. Eventually on this side the tissues break away forming an ostiolar opening. The outer perithecial wall is radial in its structure, resembling many of the Hemisphaeriales in that particular. The ascospores are 2 to several-celled and colorless or brown. *Trichothyrium* is the first described and best known genus.

Order Aspergillales (Plectascales).—This group is perhaps heterogeneous as regards certain of the included families. It shows

similarities to the Erysiphales and to the Sphaeriales and Hypocreales in its mode of sexual reproduction as well as in the conidial formation. The chief difference is the internal structure of the perithecium. In the groups just mentioned the ascogenous hyphae are of about the same length and arise from one (or more) center from which they radiate, resulting in the formation of a tuft or tufts of asci in the cavity of the perithecium or stroma, or of a hymenium at the base and sides. The thin-walled cells making up the interior portion of the stroma give way before the outgrowing asci and eventually disappear completely or nearly so or the asci and paraphyses grow up into the perithecial cavity. In the Aspergillales, on the contrary, the ascogenous hyphae are of varying lengths so that instead of arising in a tuft the asci are produced throughout the interior of the perithecium. The latter, as in the Erysiphales and Sphaeriales, consists of a firmer exterior cortex and a thin-walled interior portion. Some of these thin-walled cells are pushed aside or destroyed as the branching ascogenous hyphae grow among them so that eventually the asci appear to be imbedded here and there in the internal "nucleus" of the perithecium. Finally most of these interior cells as well as the ascus walls and the remains of the ascogenous hyphae are dissolved, leaving the ascospores loose in the perithecial cavity. True ostioles appear to be lacking. The asci are formed singly at the ends of the ascogenous hyphae, rarely by the hook method, or in chains by the transformation of successive dicaryon cells of the hypha into asci.

Conidial formation is frequently catenulate, with the apical cell the oldest, as in the Erysiphaceae. Many species occur mostly in the asexual stage, only very rarely producing perithecia. This is especially true of the very numerous species of *Penicillium* (Figure 134, A) and *Aspergillus* which form some of the commonest molds of organic matter of every kind. The details of sexual reproduction still remain to be studied for the great majority of genera. Even in those cases that have been studied much still remains to be learned, particularly regarding the behavior of the sexual nuclei. In general a straight or coiled ascogonium and coiled antherid are produced. The former may be several celled, the terminal cell perhaps corresponding to a trichogyne, or one celled. In a few cases the formation of an opening has been observed between the antherid and the tip of the oogone (or of the trichogyne), following which ascogenous

hyphae grow out of one or more of the ascogonial cells. The eminent French mycologist P. A. Dangeard has observed and figured the antherid and ascogonium in numerous species of this order. He even figures the opening from the antherid into the ascogonium or trichogyne in a few cases. He denies, however, that this is a sexual process and considers that the antherid has entirely lost its primary function as a male organ, perhaps functioning now as a nutritive organ, which he therefore calls a trophogone. In the main the mycologists, apart from Dangeard's students and associates, do not agree with him and look upon the antherid as a functional sexual organ, at least in the majority of cases where it is present. The actual observation by Schikorra and by Young of the passage of nuclei from antherid to ascogonium in *Monascus* shows the validity of this belief for that genus. On the other hand there are well authenticated cases where a coiled or straight ascogonium is produced and no organ that can be in any way interpreted as an antherid. From this ascogonium arise binucleate cells which give rise to ascogenous hyphae.

The formation of the ascus has been reported by Schikorra to take place by the hook method in *Monascus*, but this is denied by Young. In general one or more of the binucleate cells at the end of an ascogenous hypha enlarge, the nuclei fuse and the young ascus is initiated. The perithecium is formed by the growth of hyphae from near the point of attachment of the ascogonium.

In perhaps the majority of species investigated cytologically the mycelial cells and the conidia are plurinucleate. The young ascogonium and young antherid may be plurinucleate or uninucleate. It is difficult to determine which represents the more primitive condition.

Several families are recognized in this order, following Fischer in the main. Those first to be considered show the closest affinity to the Erysiphales and may well have arisen from or have given rise to that order. The sexual organs and mode of origin of the perithecium are quite similar in some of the Aspergillales to the corresponding structures of the Erysiphaceae. If the short ascogenous hyphae of the latter should become long and of various lengths, pushing in among the tissues of the central portion of the perithecium we would have the structure as it is found in the Aspergillaceae. If the central and cortical tissues of the perithecium instead of forming a firm

structure should remain more or less loose and cottony we have the Gymnoascaceae. If the perithecium should become much enlarged (up to several centimeters) with a firm cortex several layers of cells thick and a more or less permanent mass of loose central tissue (traversed by more or less well developed sterile "veins") in which the asci are scattered we have the Elaphomycetaceae. In the Onygenaceae the ascocarp is differentiated into a basal sterile portion and a somewhat larger head in which the asci are scattered in a central mass of tissue which eventually breaks up into a sort of capillitium. The Trichocomaceae and the Terfeziaceae are forms whose development is not well understood and whose relationship to the other families of the order is more or less a matter of doubt. *Myriangium* and probably several other genera rather similar in structure, forming the Family Myriangiaceae, possibly belong in this neighborhood. Miller has shown that at the apex of a stroma there arise from an ascogonium numerous branching and elongating ascogenous hyphae of dicaryon cells. These form a broad cap to the stromatic base, with no peripheral or intermingled sterile cells. The asci arise terminally on hyphae which seem to branch sympodially. They enlarge and produce eight muriform ascospores. By the weathering away of the fertile portion the asci are gradually exposed and the ascospores released. It should be noted that in 1896 Fischer placed the genus doubtfully in this order.

FAMILY ASPERGILLACEAE.—The chief genera of this family are the ubiquitous molds, *Penicillium* and *Aspergillus*, of which the commonest species are the blue and green molds found on all sorts of organic matter. Most of their species are saprophytes but a few are animal parasites, causing cases of mycosis. The small orange or yellow perithecia of a species of *Aspergillus* (Figure 77) are very frequently found on jams and various preserves, as well as on imperfectly dried herbarium specimens (herbarium mold). Usually when examined these are found to consist of nothing but a thin peridium surrounding a cavity in which will be found a large number of ascospores shaped much like a pulley wheel. Rarely a few asci will be found but usually their thin walls have completely dissolved away. In *Penicillium* perithecia are much more rarely formed and are sclerotium-like. The two genera are best distinguished by their conidiophores. In *Aspergillus* the conidiophore is swollen into a head from which radiate numerous short sterigmata bearing at the

apex of each a chain of spherical or nearly spherical, smooth or roughened conidia, or sometimes producing secondary sterigmata which bear in their turn the chains of conidia (*Sterigmatocystis*, Figure 134, *B*). In *Penicillium* the conidiophore branches several times without enlarging, the terminal portions lying more or less parallel and bearing one to three or four sterigmata with chains of conidia (Figure 134, *A*). *Citromyces* is much like *Penicillium* but the conidiophores or their branches are somewhat thickened. The chief

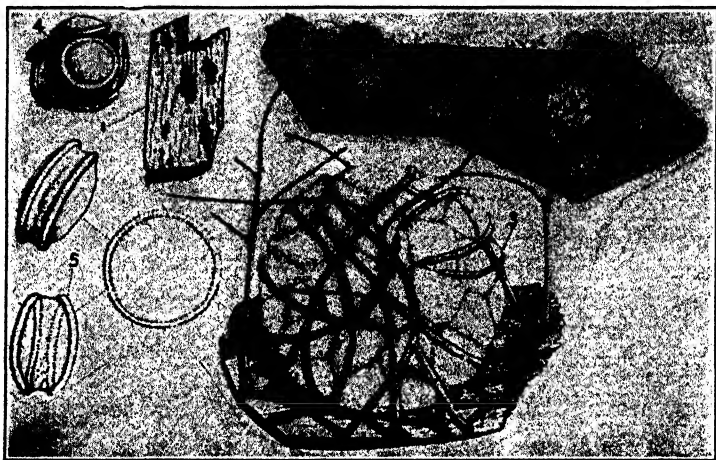


FIG. 77.—Aspergillales. *Aspergillus* sp. (After Ellis and Everhart, 1892.)

distinction is a biological one, viz. the production of large quantities of citric acid when grown on a medium containing sugar. *Monascus* is usually distinguished by its red or pink mycelium. The conidia are in short chains. The mature perithecium consists of one or two layers of cortical cells around a cavity enclosing the numerous ellipsoid or globose ascospores, the interior perithecial tissues and the walls of the 8-spored asci having dissolved rather early. This was first interpreted as a single many-spored ascus, hence the name *Monascus* (meaning one ascus). One species of *Monascus* is the "pink mold" found in ensilage that was put into the silo in too dry condition. Other species are used in the Orient for the fermentation of rice in the preparation of alcoholic beverages.

Sexual reproduction has been studied in several members of this family. Both Schikorra and Young have studied the genus *Monascus*. In this genus a slender plurinucleate antherid is produced at

the end of a hypha. Sympodially from the cell below arises the ascogonial branch which bends so as to lie parallel to or to coil somewhat around the antherid. A basal cell cuts this off from the main hypha and soon an apical trichogyne cell is set off by another septum. Trichogyne and oogone both contain several nuclei. An opening appears between the trichogyne and antherid through which the antherid nuclei pass, the trichogyne nuclei having previously disappeared. The septum between trichogyne and oogone dissolves out and the male nuclei pass into the latter, the septum then being regenerated. The nuclei pair by twos in the oogone but fusion of these pairs has not been observed. In the mean time hyphal branches arising from just below the oogone form the beginning of the perithecial wall which is one or two layers of cells thick. From the base of the fertilized and enlarged oogone grow several ascogenous hyphae, each of several dicaryon cells. The apical and second and third cells may develop into asci, each with 8 ascospores. Ascus walls and the remainder of the ascogenous hyphae and of the oogone and antherid dissolve and leave the ascospores free in the perithecial cavity. In *Aspergillus herbariorum* de Bary and later Miss Dale report that a tightly coiled ascogonium is formed, at first one celled but soon dividing into several multinucleate cells. An antherid arising from lower down or from another branch climbs up the side of the coiled ascogonium. A fusion of antherid and ascogonium has not been observed and possibly does not occur. It is not certain that this is really an antherid. Possibly it is one of the investing hyphae. Soon the middle cells of the ascogonium divide into binucleate cells from which arise the branched ascogenous hyphae, while from the cells supporting the ascogonium arise the hyphae which form the perithecium with a cortex of one layer of polygonal cells and filled with thin-walled interior cells. In the species of *Penicillium* called by Brefeld *P. crustaceum*, this mycologist reports the formation of short coiled antherid and ascogonium from adjacent cells of the same hypha. These fuse at the apex and give rise to a several celled structure from which branch out the ascogenous hyphae while around them a dense sclerotium-like perithecium develops. The nuclear behavior has not been followed. In *P. vermiculatum* Dangeard reports the formation of a long straight multinucleate ascogonium around which coils a slender antheridial hypha with an enlarged uninucleate

antherid at the apex. This fuses with the ascogonium and the male nucleus may pass into the latter or may remain in the antherid. The ascogonium divides into binucleate cells from which arise the ascogenous hyphae. Dangeard reports that the male nucleus is not functional.

FAMILY GYMNOASCACEAE.—The species of this family are mostly saprophytic on animal matter such as feathers, dead animal bodies, excrement, etc. A number of skin parasites of Man and other animals appear to belong in this family. The conidia are mostly single, not catenulate. In *Ctenomyces* Eidam described a multinucleate ascogonium coiled around the straight multinucleate antherid. Passage of nuclei from the latter to the former was observed. The ascogonium soon divides into numerous short binucleate cells each of which produces a more or less coiled ascogenous hypha. During this time the nearby hyphae have formed a loosely woven perithecial wall around the developing ascogenous hyphae. In *Gymnoascus reessii* the union of antherid to the tip of the coiled ascogonium was observed by Baranetzky. Later Dale observed the passage into the ascogonium of several male nuclei. The ascogonium divides into a number of cells each of which produces ascogenous hyphae. The perithecial wall in this genus is a mass of loosely interwoven hyphae (Figure 78).

FAMILY ELAPHOMYCETACEAE.—These fungi are subterranean and probably saprophytes. The ascocarps are large, up to 2 or 3 cm. in diameter with a very thick peridium, usually hard and roughened externally, the central portion consisting of the ascogenous hyphae and asci and the thin-walled central cells of the ascocarp, traversed radially by the "veins" which probably are conductors of food stuffs. The cell walls of the central portion dissolve leaving the numerous ascospores free in the center of the ascocarp. Clemencet reports that in *Elaphomyces* no sexual organs are to be found but that in *Ascocladeroderma* (a segregate of that genus) a stout ascogonial filament coils around a straight antherid. The latter is sexually functionless, according to this author. From the ascogonium arise branching ascogenous hyphae which produce at their tips rectascous asci, i.e. the cell elongates and the nuclei fuse, without any curving or hook formation. This is in agreement with the observation as to ascus formation in most genera of the order. In *Mesophellia* Dodge observed two multicellular threads coiled about each other

but did not follow out the subsequent stages of sexual reproduction. About 20 to 30 species in 2 genera are reported by Dodge from the temperate regions of Europe and North America.

FAMILY ONYGENACEAE.—This contains a few species in the genus *Onygena*, found mostly in temperate Europe and North America. They grow on old feathers, hair, hoofs, ham, felt and other animal

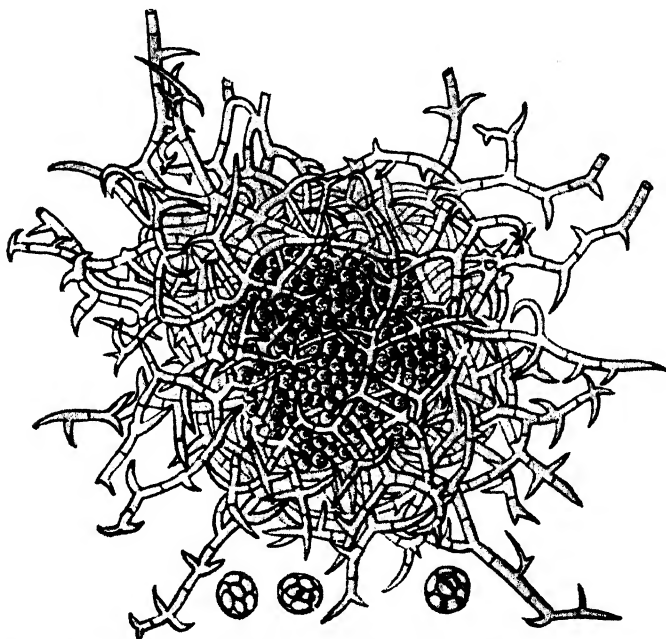


FIG. 78.—Aspergillales. *Gymnoascus reessii*, perithecium and asci. (After Brefeld, 1891.)

matter. The ascocarps are a few millimeters up to 1 or 2 centimeters tall, consisting of a stalk and somewhat enlarged head within which the asci are scattered in the manner characteristic of this order. The tissues break up into a sort of capillitium.

Order Saccharomycetales.—This order represents, in the opinion of the author, the ultimate degree of simplification in the Class Ascomycetae. On the other hand it must be noted that for many eminent mycologists, such as de Bary, Brefeld, Gäumann, Dangeard, Atkinson, and others, the members of this order are looked upon as primitively simple, representing almost the first steps

in the development of the Ascomyceteae from the Phycomyceteae. To agree with this theory the arrangement of the orders of this class should be reversed, placing this order first and the very complex Pezizales and their allies last.

The fungi making up the Saccharomycetales are usually divided into two groups, Family Endomycetaceae and Family Saccharomycetaceae (the Yeasts) with a third family, the Ascoideaceae probably belonging here. The latter family has polysporous asci and the other two have eight or four or fewer-spored asci. The Endomycetaceae and Ascoideaceae possess a filamentous mycelium consisting of uninucleate or more often plurinucleate cells. Conidia are usually formed by the breaking up of part of the mycelium into more or less rounded cells or oidia. When placed in nutritive media of considerable concentration the mycelium has a tendency to break up into its individual cells and grows in the manner of a yeast. The Saccharomycetaceae under normal conditions grow as yeasts, i.e. the mycelium breaks up into individual cells which multiply by simple fission or by budding, separating soon after dividing. Under special cultural conditions longer hyphae may be formed which show great similarity to those of the Endomycetaceae.

FAMILY ENDOMYCETACEAE.—Fungi with a well developed vegetative mycelium of uninucleate or more often plurinucleate cells. Asexual reproduction mostly by the breaking up of portions of the hyphal branches into oidia. Sexual reproduction occurs in *Eremascus* by the apical fusing of an antherid and ascogonium that may be indistinguishable in appearance. They usually arise from adjacent cells. Each structure is uninucleate, whether the mycelial cells are uninucleate or plurinucleate. At the point of fusion a zygote cell is formed which perches on top of the two sexual structures. In it the two nuclei fuse and then undergo division resulting in the formation of eight nuclei around each of which in the usual manner, an ascospore is formed. In *Endomyces magnusii* the antherid and oogone are unequal and the male nucleus passes into the oogone where nuclear fusion occurs and the oogone elongates and becomes the ascus. The latter is 4 spored. In some species of *Endomyces* no antherid is formed and a four-spored ascus is formed apogamously on the end of a hypha or of a short branch. In some species the ascospores are round with one flattened side with a projecting rim, resembling a round topped hat, in others they are ellipsoidal.

Moore has studied *E. capsulatus*, pathogenic in Man. Isogamy, heterogamy and parthenogenesis may be present in the same culture. The conjugating cells (gametangia) contain several nuclei, but only one from each cell functions, apparently the one nearest the apex of the cell. This is of significance in connection with the Ascoideaceae.

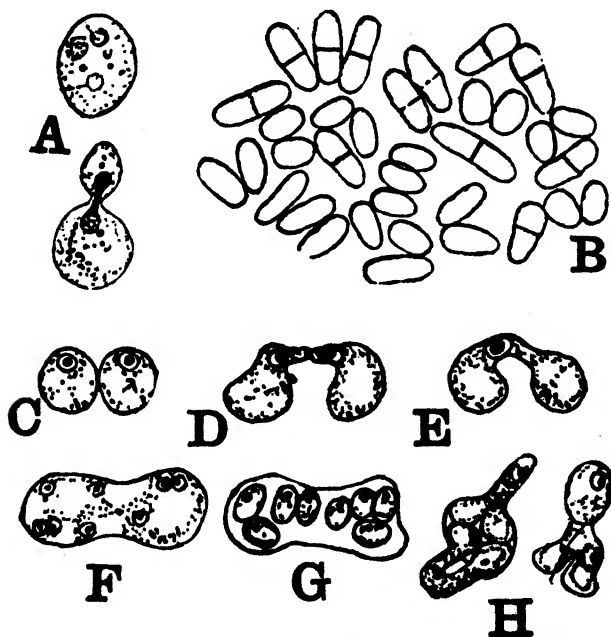


FIG. 79.—Saccharomycetales. A, A budding yeast, *Saccharomyces cerevisiae*; B, a fission yeast, *Schizosaccharomyces octosporus*; C–G, stages of conjugation and formation of ascospores in the foregoing species; H, conjugation of ascospores within ascus, *Saccharomyces ludwigii*. (After Guilliermond, 1912.)

FAMILY SACCHAROMYCETACEAE. (sometimes divided into three families, Saccharomycetaceae, Schizosaccharomycetaceae and Zygosaccharomycetaceae).—The Yeasts. These fall into two groups in accordance with their mode of vegetative growth: the fission (Figure 79, B) and the budding yeasts (Figure 79, A). In the former each cell divides by fission into two equal parts while in the latter small buds grow out of the larger cells and gradually increase in size until they are equal to the cells from which they budded. Fabian and McCullough have shown that by growing yeasts in certain cultural conditions or by the addition of lithium salts to the culture

media the vegetative cells may be induced to break up into minute cells much different in pathogenicity, ability to cause fermentation, etc. These eventually on proper media will resume the normal size and characters of the original cells. This is of especial interest as it shows a parallelism in behavior to that demonstrated by Hadley and others to occur in true Bacteria. In *Schizosaccharomyces* (a fission yeast) and *Zygosaccharomyces* (a budding yeast) Guilliermond and others have shown that two vegetative cells in contact under the right environmental conditions may fuse and the two nuclei unite (Figure 79, C-G). The zygote nucleus divides and forms mostly 4 or 8 nuclei, sometimes fewer, around each of which an ascospore forms. The fusion of the two cells may be complete or only by means of a slender tube. In the latter case the ascospores may all be in one cell or may be distributed between the two cells which remain connected by a slender neck. The conjugating cells may be unequal in size as Guilliermond has shown for *Z. pastorii*. In *Zygosaccharomyces chevalieri* a vegetative cell may bud and the large mother cell and small daughter bud may then unite by a slender conjugation tube, eventually forming four ascospores. In *Saccharomyces ludwigii* conjugation occurs between the ascospores in pairs within the ascus (Figure 79, H), without any prior fusion of vegetative cells. Probably each cell of the latter contains a diploid nucleus, meiosis occurring as the ascospores are being formed. In *Saccharomyces cerevisiae*, the ordinary bread yeast, as well as in many other yeasts the asci develop parthenogenetically from vegetative cells in which the single nucleus divides successively to form the four nuclei of the four or fewer ascospores. In perhaps the majority of the yeasts the ascospores are ellipsoidal but in some species, as in some of the Endomycetaceae, they are flattened on one side and hat shaped.

Zender proposes a classification within this order quite different from the conventional one just given. Regardless of the degree of development or reduction of the mycelium (to one-celled yeast forms) all species with an equatorial or basal projecting ridge on the ascospore, with 4 or fewer ascospores to the ascus, and with uninucleate vegetative cells are placed in the Endomycetaceae while the Ascoideae include filamentous forms with multinucleate cells and polysporous asci, the ascospores being hat-shaped as in the preceding family. The Eremascaceae are yeast-like or possess an extensive

mycelium of plurinucleate cells and produce 4-8 ascospores in the ascus, these being ellipsoidal or globose. The Schizosaccharomycetaceae, with cells dividing by fission, and Saccharomycetaceae, with budding cells, form the true yeasts. These have ellipsoidal or globose ascospores. *Nematospora*, with needle-shaped ascospores Zender places in Hansen's family Non-saccharomycetaceae. Another family, Pichiaceae, is also recognized. Its ascospores are irregular, without a rim. On proper media true hyphae may be formed.

The yeasts have considerable economic value. The common bread yeast (Figure 79, A), a budding yeast, when grown in sugary media ferments the sugar into CO₂ and alcohol. In the baking of the dough the bubbles of CO₂ expand and thus the bread is made light. This and other species are also used for the production of alcohol, either for beverage or industrial purposes. The genus *Nematospora*, first recognized by Peglion, consists of yeasts whose ascospores are filiform. Species of this genus cause rot in the tomato fruit (*Lycopersicum*) and a disease of the bolls of cotton (*Gossypium*) and of other plants. Guilliermond's studies of *N. gossypii* and of *N. coryli* seem to demonstrate that these develop their ascospores parthenogenetically. The former species is normally filamentous, of plurinucleate cells, the latter is mostly yeast-like, more rarely filamentous. The ascus is more or less spindle shaped, several in a row in the second species. It contains 1, 2, 3, or 4 or more nuclei which divide twice, forming as many groups of four nuclei around each of which is formed an ascospore. This is long spindle shaped, one end being rather firm walled, the other end thinner walled and tapering into a long flexuous appendage resembling a flagellum, probably an organ of adhesion. Some yeasts are present in the alimentary canals of Man and other animals. Many occur in the soil and others in overripe fruits, etc. Some yeasts cause diseases of the skin.

FAMILY ASCOIDEACEAE.—This family contains a very few species of two genera, *Dipodascus* and *Ascoidea* which have some points in common with the Endomycetaceae but differ from the fungi of that family in some very important characters. Perhaps further study will lead to their transfer to a distinct order, but for the present they would perhaps better remain in the Saccharomycetales. They are of little economic importance but possess great interest because they are considered by many mycologists to represent an intermediate

stage between the Class Phycomyceteae and the Class Ascomyceteae. They are found in the plant slimes or sap exuding from wounded surfaces. Whether they are the cause of such slime flux or are merely saprophytes has not been definitely settled.

The two genera agree in the production of mycelium with multinucleate cells and in the fact that the uniting sexual organs are multinucleate, and the resulting ascus multispored. In the two other families of the order the sexual organs are uninucleate and the asci mostly 4 or 8 spored.

Dipodascus albidus was collected by Lagerheim near Quito, Ecuador, in the gummy exudate from a cut surface of one of the Bromeliaceae. It was brought into cultivation and has been studied in culture by him, Juel and other capable mycologists. The mycelial cells are plurinucleate. Asexual reproduction occurs by the breaking up of a portion of the mycelium into oidia, each containing several nuclei. Sexual reproduction occurs early. From adjacent cells of the same hypha, close to the intervening septum, there arise short, plurinucleate branches which become separated from the parent hypha by the formation of septa. These branches meet and an opening forms at the point of contact. One nucleus from each organ becomes more conspicuous and these two "privileged" nuclei approach and fuse, either in the connecting bridge or, more rarely, a little to one side of it in the larger organ (the oogone). From this point (i.e. either from the bridge or from the oogone) a multinucleate extension grows upward, parallel to the original axes of the sexual organs. In this elongated structure (or ascus, it may be called) the fusion nucleus undergoes repeated division while the numerous other nuclei gradually degenerate until the only nuclei present seem to be those descended from the fusion nucleus. Probably the first two of these nuclear divisions are meiotic. When the nuclear divisions have ceased a thin layer of cytoplasm gathers around each nucleus. These at first have no wall but are separated from each other by the epiplasm. They increase in size rapidly and then secrete walls, becoming round or ellipsoid spores. The ascus tapers gradually at its apex, the ascospores moving up into this slender apical portion. The apex ruptures and the numerous ascospores and the surrounding epiplasm emerge as a large drop which dissolves in the dew or rain, thus permitting the distribution of the spores.

Ascoidea rubescens is found in the sap exuding from wounds in trees, perhaps more frequently the beech (*Fagus*). Vegetatively it is quite similar to *Dipodascus*. The conidia are lateral or terminal cells, and are not produced by the breaking up of the hypha as in *Dipodascus*. The ascus arises terminally on a branch as a multinucleate cell. Varitchak has demonstrated that two of the nuclei (privileged nuclei as in *Dipodascus*) enlarge and fuse (Figure 80, B, C). From this point onward the development of the

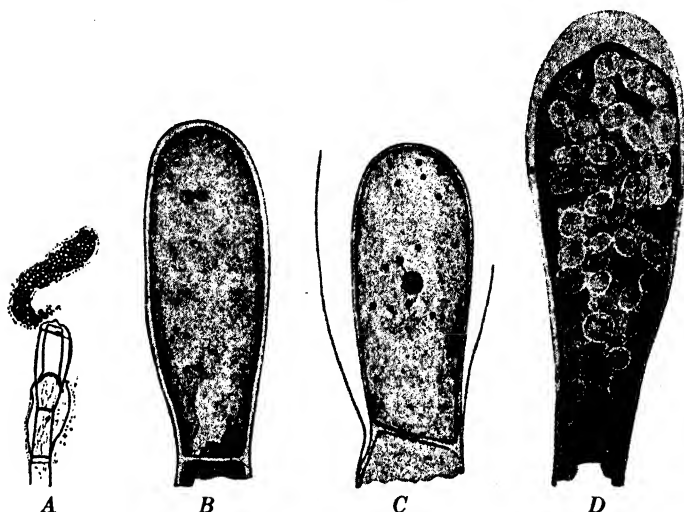


FIG. 80.—Saccharomycetales, *Ascoidea rubescens*. A, proliferated asci and escaped ascospores; B, young ascus with two privileged nuclei about to unite; C, zygote nucleus large, other nuclei degenerating; D, mature ascospores surrounded by epiplasm. (A after Miss Walker, 1931; B–D after Varitchak, 1931.)

ascus is essentially as in *Dipodascus*. The descendants of the fusion nucleus become the nuclei of the ascospores while the other nuclei gradually disappear (Figure 80, D). Varitchak believes that the first two divisions of the fusion nucleus accomplish meiosis. The numerous ascospores are flattened on one side and hat-shaped as in some species of both Endomycetaceae and Saccharomycetaceae. The ascus ruptures at the slightly tapered apex and the ascospores and epiplasm escape in a long worm-like mass, the discharge being aided by the growth of a new cell up into the old ascus (Figure 80, A). This new cell becomes another ascus. The process may be repeated 10 or 12 times, as is the case in the zoosporangial development in *Saprolegnia*. Miss Walker reports that the germinating ascospores

frequently unite by twos, the further growth of the new mycelium extending from this conjugation tube. This should be compared with the phenomenon of union of gametes in *Spermophthora* below.

Here must be considered *Spermophthora gossypii* a form whose true relationships are far from settled. It was discovered and described by Ashby and Nowell who determined it to be the cause of stigmato-mycosis of seeds of cotton (*Gossypium*) in India. Guilliermond studied it culturally and cytologically, reporting the following:

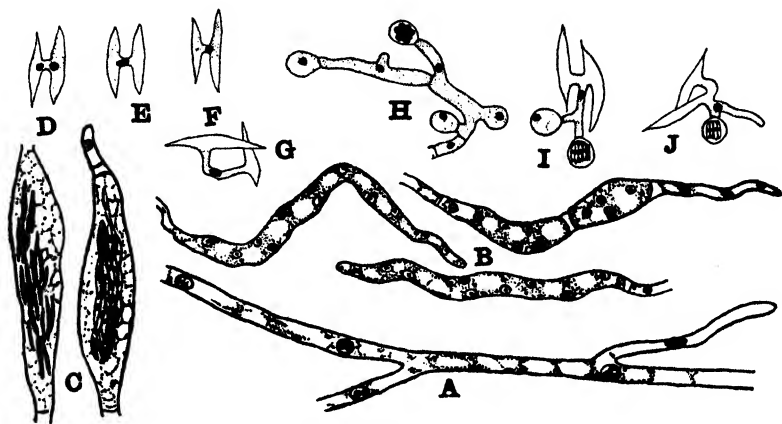


FIG. 81.—*Spermophthora gossypii*. A, gametophytic, coenocytic mycelium; B, developing gametangia; C, mature gametangia with gametes; D–G, uniting gametes; H–J, sporophytic mycelium bearing asci. (After Guilliermond, 1928.)

The germinating ascospores give rise to a non-septate, coenocytic, dichotomously branching mycelium with apical growth (Figure 81, A). The apices of the branches may continue to grow while the older parts die and are cut off by callose plugs as in some Phycomycetae. A short distance back from the hyphal tips the mycelium forms spindle-shaped swellings, the gametangia, which become separated from the usually short tip cell by a cross wall, another septum setting this swelling off from the main portion of the mycelium (Figure 81, B). These gametangia are at first 4 to 8 or 10 nucleate. The nuclei divide twice simultaneously. The resulting nuclei and most of the cytoplasm form a dense axial strand surrounded by a vacuolate epiplasm. The axial portion divides into fusiform, uninucleate cells (Figure 81, C) which enlarge at the expense of the epiplasm. The rupture of the gametangium wall

permits the non-motile gametes to escape. Whenever two lie in contact they unite by a conjugation tube within which, usually, the two nuclei unite (Figure 81, *D-G*). From this conjugation tube there grows out a rather limited, branched mycelium of uninucleate cells. The ends of the hyphae enlarge and are cut off by a septum and become spherical asci (Figure 81, *H-J*). The nucleus divides three times and around each nucleus is formed a more or less lemon-shaped ascospore. As the eight ascospores enlarge they use up the epiplasm. They usually remain in a rather compact bundle even after the ascus wall disappears. Rarely a gamete germinates parthenogenetically to form a septate mycelium bearing apparently normal asci. Although the cytological details could not be made out Guilliermond believes that the first two divisions of the ascus nucleus are meiotic so that the fungus shows an alternation of a gametophyte with haploid nuclei and a sporophyte with diploid nuclei. He believes that the fungus occupies a position intermediate between the Phycomycetes and Ascomycetes. Comparing *Spermophthora* with higher Ascomyceteae (e.g. *Pyronema*) he considers its sporophytic stage with uninucleate cells and diploid nuclei to be homologous with the system of ascogenous hyphae with cells containing pairs of haploid nuclei. In the former the single diploid nucleus in the ascus divides to form the nuclei of the ascospores, in the latter the two haploid nuclei unite, then divide to form the nuclei of the ascospores. In both, the ascospores with their haploid nuclei give rise to a gametophyte. In *Spermophthora* the gametangia produce individual gametes which are set free and unite; in the higher Ascomyceteae two gametangia (antherid and oogone) unite but the contained nuclei do not unite now but wait until the ascus is formed. On the basis of this homology Guilliermond considers the Saccharomycetales to represent a lateral offshoot in which the union of gametangia has become established but in which the sporophytic phase has undergone reduction to a single ascus. Thus *Dipodascus*, *Ascoidea*, *Endomyces*, etc. are not in the line of evolution to the higher Ascomyceteae which arise more directly from forms intermediate between them and *Spermophthora*.

On the other hand the multinucleate sexual organs of *Dipodascus* have been compared by many mycologists to the two gametangia of Mucorales and the ascus arising at their apex after fusion has been compared to a zygosporangium which at once takes on a sporangial

function. It is known that in some of the Mucorales but one nucleus from each multinucleate gametangium is specialized to function as a sexual nucleus. Thus Dangeard, Gäumann, Atkinson, Fitzpatrick, and many others look upon *Dipodascus* as a transition form from the Phycomyceteae to the Ascomyceteae, the polysporous ascus being considered a further indication of primitiveness. Their theory would involve a reduction of this polysporous condition to the 8 or 4 spored condition found in *Endomyces*, and other Saccharomycetales. This is supposed to have been followed by a branching of the zygote to produce several asci, thus leading to the structures found in the higher Ascomyceteae.

The formation of numerous ascospores in the ascus of *Dipodascus* or of *Ascoidea* is not of itself an indication of primitiveness of character, for in the Sphaeriales, certainly not a primitive order from any standpoint, very numerous ascospores are found in some of the Diaporthaceae, while Ames reports, in a letter to the author, that he has found a species of *Pleuraea* with 512 ascospores in the ascus. *Thelebolus*, probably belonging to the Pezizales, has over 1000 ascospores in its single ascus. It is only in connection with other features that polyspory of the ascus can be considered primitive.

Attention must be drawn to the fungus *Pericystis*, the cause of "chalkbrood" in bee hives. The systematic position of this fungus has been in doubt. Fitzpatrick places it among the doubtful Phycomyceteae. Varitchak has studied the life history and nuclear behavior of *P. apis* and concludes that this organism is a primitive Ascomycete related to *Dipodascus* and *Ascoidea* but far nearer the Phycomycetous ancestors of the class. The mycelium as in *Ascoidea*, contains chitin, not cellulose. As in that fungus it is septate, with multinucleate segments, the young septa being centrally perforated, permitting flowing of cytoplasm from segment to segment. Mycelia are of two sexes, the fungus being heterothallic. When they come into contact multinuclear gametangia arise, separated by a septum from the main hypha, resembling at first the early stages of conjugation in *Mucor*. The female gametangium enlarges and the male gametangium sends a conjugation tube into it. Numerous male nuclei and some cytoplasm enter the oogone, whose nuclei divide several times as do the introduced male nuclei. Many nuclei of both sexes degenerate but many uniting nuclei are found. Around each such zygote nucleus is organized a mass of cytoplasm,

called by the investigator an egg. There is no cell wall between this "egg" and the rest of the protoplasm. The number of such zygote nuclei and eggs varies, usually being large, but varying in number down to only one, in rare cases. Each zygote nucleus divides several times and the egg cytoplasm undergoes cleavage until as many spores are formed as there were nuclei. Spore walls are formed and within the gametangium are now found as many spore balls as there were uniting pairs of nuclei. Varitchak calls each ball of spores an ascus and the whole structure a "synascus." By reduction of the number of uniting nuclei and resulting spore balls a condition would be attained as in *Dipodascus* with a "hemiascus." By reduction of the number of nuclei in the uniting gametangia to one in each, as in *Endomyces*, a true ascus results from their union.

In the author's view the Saccharomycetales represent a further development, with increasing simplification, from the Aspergillales. In that order we see the tendency toward reduction of the perithecium from a firm structure as in the Aspergillaceae to a loose tufted mass of hyphae in the Gymnoascaceae. Carry this further and the perithecium disappears while at the same time the number of asci resulting from the union of antherid and oogone has become reduced to one. This has already been observed in the Erysiphales in the genera *Podosphaera* and *Sphaerotheca* and in the Pezizales in *Thelebolus*. Frankly, the existence of *Spermophthora* can not be accounted for as a reduced form of the Class if its described life-history is correct.

SUMMARY OF THE CLASS ASCOMYCETEA

This class consists of fungi exceedingly different in habits and degrees of development of the mycelium. The latter may be very extensive or reduced (in the Yeasts) to single cells; the mycelial cells may be uninucleate (apparently more frequently so) or plurinucleate. The cell wall usually consists of a framework of chitin, which appears to be absent in some forms, and whose presence or absence in the supposed intermediate groups needs further investigation. On this is deposited true cellulose or more often some other carbohydrate (callose in many cases) combined with or overlaid by certain fatty acids and with protein-pectic compounds. Asexual reproduction is by the formation of certain cells as conidia or by the breaking up of a whole hypha or of a portion of it into oidia. Sexual reproduc-

tion (in the author's opinion) is primitively the union of non-motile, uninucleate, sperms with a receptive organ (trichogyne, comparable functionally with and probably homologous to the trichogyne of the Florideae) which is an extension of the oogone or the terminal cell or cells of a row, one of which is the functional oogone. The male nucleus eventually reaches the oogone and unites there with the female nucleus. The zygote nucleus divides and the resultant nuclei pass out into hyphal outgrowths from the oogone (ascogenous hyphae), in which the nuclei are usually in pairs. In the terminal cells the paired nuclei unite, divide by meiotic division and the ascospores are produced. In many cases, representing perhaps the majority of species, nuclear union fails to occur in the oogone so that the only union is that in the ascus. Even the antherid may disappear in which case the female nuclei pair off but do not unite until the ascus is reached. The union of sperm to trichogyne gives way to direct union of trichogyne with antherid and to the gradual reduction and disappearance of the trichogyne. As is often the case in the Florideae, adjacent vegetative tissues usually form a protective structure (apothecium or perithecium) about the developing asci. These structures undergo modification and reduction until eventually they disappear entirely in the Saccharomycetales.

Whether the primitive Ascomyceteae emerged from their aquatic ancestral habitat as parasites on insects (Laboulbeniales) or algae (the Lichens) or whether they were first saprophytic and acquired the parasitic habit on these organisms later is a matter of conjecture. It is noteworthy that these two groups of fungi are those in which the trichogyne and non-motile sperms are most generally formed, though they also appear in some of the more primitive Pezizales and Sphaeriales as well as in the Rusts (Uredinales) to be taken up in the next chapter.

It is only fair to point out that if the Saccharomycetales or *Spermophthora* are considered primitive, the line of evolution is no more broken than in the opposite direction. From these forms would arise the Aspergillales, Erysiphales, Sphaeriales, Pezizales, Lecanorales (omitting reference to some of the smaller orders). The fertilization of the trichogyne by a non-motile sperm is, by this theory, looked upon as a substitution of a conidium for an antherid. The Florideae would then be considered as not in the least related to this class. It is noteworthy that the serum reaction studies of

Mez seem to show no connection between Red Seaweeds and Ascomyceteae and some connection between Phycomyceteae and Saccharomycetaceae.

Both theories have their difficulties. The composition of the cell wall is more like that in some of the Phycomyceteae (Mucorales and Entomophthorales). The formation of ascospores surrounded by an epiplasm has no homologue in the sporangium of the Phycomyceteae or in the spore-fruit of the Florideae. The mycelium of the Phycomyceteae consists typically of coenocytic tubes, that of the Ascomyceteae is typically cellular, of uninucleate cells, as is true of the majority of the Florideae; but in the Saccharomycetales it is often composed of multinucleate cells, reminiscent of the Phycomyceteae.

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CHAPTER X

CLASS TELIOSPOREAE: THE RUSTS AND SMUTS

The Class Teliosporeae corresponds to Dietel's limits of Subclass Hemibasidii of the Class Basidiomyceteae, in the second edition of Engler and Prantl's *Die Natürlichen Pflanzenfamilien*. These fungi have been sometimes called the Brand Fungi. Usually the two orders Uredinales and Ustilaginales have been considered to be more or less closely related. They were placed close together by Fries and by Plowright and by most of the later botanists. Bennett and Murray separated the orders placing the Ustilaginales as part of their Class Zygomycetes while the Class Uredineae was placed between the two classes Ascomycetes and Basidiomycetes, the affinities being considered as lying with the former. Because of the fancied resemblance of the teliospores of Rusts to asci Charles E. Bessey was inclined to include the Uredinales and Ustilaginales in the Class Ascomyceteae, a position from which he receded when the cytological phenomena of these groups became better known. Saccardo in 1891 included them in his group Hypodermmeae. That they are rather closely related to the true Basidiomyceteae the studies of Brefeld and the cytological investigations of Sappin-Trouffy, Harper and others leave little doubt. That they stand apart from the majority of families of that class is equally certain. The author (following Charles E. Bessey) believes that the differences are sufficiently great to warrant placing them in a separate class, a position that does not deny the relationship of the two groups, but leaves each class much more homogeneous.

The fungi of this class are parasitic. In the Order Ustilaginales some of the species are capable of saprophytic growth in media rich in food; in the Uredinales growth is strictly parasitic and the fungi have never been cultured except on the living tissues of the host. The mycelium is long, slender and branching, growing intercellularly within the host. In the majority of cases studied occasional or frequent haustoria are produced. The cells of the mycelium are

mostly uninucleate in one stage of development (monocaryon stage) and binucleate in the remainder of the life cycle (dicaryon stage). As the cells of the mycelium divide the two nuclei divide simultaneously so that one daughter nucleus of each of the original nuclei will be found in each of the two daughter cells. This is the type of nuclear division named "conjugate division" by Poirault and Raciborski. Finally, on the dicaryon mycelium are produced certain larger cells, usually terminal to a hypha or its branches, which become thicker walled. Within these cells the two nuclei unite to form the only diploid nuclei in the life cycle of the fungus. These cells are the teliospores. In the Ustilaginales (Smuts) these are often spoken of as "chlamydospores," a misuse of this name which should be applied only to vegetative cells which become filled with food and develop thick walls to permit survival over winter or through other unfavorable environments. In true chlamydospores there is no nuclear fusion and their germination is in the manner usual for asexual spores.

Plowright recognized the essential homology of the teliospores in the two orders. The teliospores have a typical manner of development. The diploid nucleus divides by meiotic division into four nuclei in the teliospore or more often the exospore ruptures and a thin walled hypha grows out into which the diploid nucleus passes. The meiotic divisions then take place in this hypha instead of in the body of the teliospore. In some cases the nuclei divide once or twice more resulting in the production of 8 or 16 or even more nuclei. The short hypha which emerges from the teliospore is the promycelium. It may remain non-septate but more often becomes transversely septate into four cells. From each of these cells is produced a sessile or stalked sporidium or several such sporidia. From the non-septate promycelium four to sixteen or more sporidia bud out at the apex.

Many writers e.g. Arthur, Gäumann, etc., apply the names basidium and basidiospores respectively to what are called here promycelium and sporidium. In the author's opinion the differences are sufficient to make desirable the retention of the latter (and for the Uredinales the older) names. As will be seen in the discussion of the Basidiomyceteae the typical basidium, like the teliospore and most asci, is a terminal cell of a series of dicaryon cells. In this terminal cell the nuclei unite and undergo meiotic divisions and then

from the basidium itself there bud off the basidiospores into which the nuclei pass. In the teliospores there are the similar fusion of nuclei and the reduction divisions, but the spores arise from a hypha (promycelium) which grows out of the teliospore. It is quite probable that one of these processes has been evolved from the other or that both had a common origin. In any case the typical basidium is not the exact homologue of the promycelium but of the teliospore and the promycelium together. However in certain forms with atypical (and perhaps primitive?) basidia the latter are much more like the structures found in the Teliosporeae.

Asexual reproduction is known in both the Uredinales and the Ustilaginales. In the latter it occurs by means of colorless, often spindle-shaped or sickle-shaped conidia which are uninucleate or binucleate. The latter arise only from dicaryon mycelium but the uninucleate conidia may arise from either monocaryon or dicaryon mycelium. They arise on very short conidiophores, or rather sterigmata, from the sides of the mycelial cells. They are usually in the true sense of the words "repeating spores" for they produce the same type of mycelium as that from which they arose, except in the case of uninucleate conidia from dicaryon mycelium. These give rise to monocaryon mycelium. These conidia are mostly produced on the saprophytic mycelium, but in some species are produced on sterigmata which emerge through the epidermis of the living host. In the Uredinales (Rusts) the urediniospores (uredospores) are dicaryon repeating spores and are, therefore, true conidia. There are no monocaryon repeating spores in the Rusts. The aeciospores (aecidiospores) are the result of a sexual fusion involving cells but not the nuclei. They bridge over the step from the monocaryon phase to the dicaryon phase. They are not strictly homologous to ordinary conidia but yet show great resemblance to the urediniospores.

Sexual reproduction occurs in two usually widely separated steps: the union of two monocaryon cells to initiate the dicaryon mycelial phase and eventually the union of the nuclei in the teliospores to form a diploid nucleus. The points at which the dicaryon phase may be initiated are quite variable in the Smuts but much more definite in the Rusts. The details will be taken up in the discussion of the respective orders.

Order Uredinales. The Rusts.—These form a group which manifests a very high degree of evolutionary development in many directions. The 7000 or more species are all strict parasites of Ferns (Pteridophyta), Conifers (Strobilophyta) and Flowering Plants (Anthophyta). Not only are the Rusts strict parasites but in many cases they are highly specialized into biological races which are confined to certain species of a host genus or even to special agricultural varieties of a host species just as is the case in *Erysiphe graminis*. In Europe Eriksson was the first to make extensive studies of the specialization of species into physiologic races confined to related species. He was followed by numerous other investigators on that continent. In the United States Carleton was the first to follow up Eriksson's work, followed by Freeman and by Stakman and others. The study of the physiologic forms on special agricultural varieties of these species has been carried out in this country very extensively by Stakman and various collaborators. For example in *Puccinia graminis tritici* the physiological race that attacks common wheat (*Triticum aestivum*) and durum wheat (*T. durum*) over one hundred physiological forms have been distinguished by means of their behavior on ten or more differential varieties of wheat. Similar physiologic forms have been found in leaf rust of wheat (*P. rubigo-vera tritici*) by Mains and Jackson in the United States and Scheibe in Germany, also in maize rust (*P. sorghi*) etc.

With one or two exceptions the teliospores are produced within the tissues of the host and remain internal or break out through the epidermis separate and free or united together in a waxy mass or attached by stalks. The sporidia are capable of wind distribution but are short-lived and delicate so that they can be carried only short distances in a living condition. Two other spore forms are usually produced, the aeciospores and the urediniospores, both of which are relatively thick-walled and capable of remaining alive while being carried many miles by the wind (many hundreds of miles in some cases).

The mycelium occurs in two well marked alternating phases, the monocaryon (Figure 82, A) and the dicaryon phase (Figure 82, E; 84 D). Clamp connections (to be described in detail in the chapter the Basidiomyceteae) have been reported by Voss on the mycelium in the aecial phase but their existence appears doubtful. Haustoria

are frequent, sometimes small and spherical, sometimes large and branched and often partially surrounding the nucleus of the host cell. They are uninucleate or binucleate, according to the type of mycelium producing them. Colley showed for the White-Pine Blister-rust (*Cronartium ribicola*) that the haustorium (Figure 82, A)

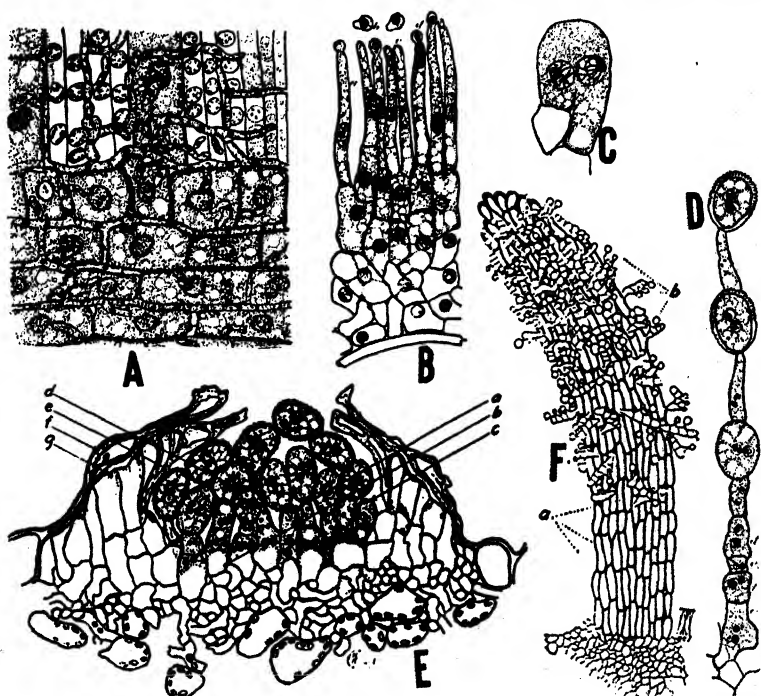


FIG. 82.—Uredinales. *Cronartium ribicola*. A, monocaryon mycelium in tissues of *Pinus strobus*; B, portion of spermagonium; C, union of two cells to form basal cell of aecial chain; D, aecial chain; E, uredinial sorus in leaf of *Ribes*; F, telial column on leaf of *Ribes*. (After Colley in Journ. Agr. Res., 1918.)

does not usually truly penetrate the protoplast of the host cell but causes an invagination. Miss Rice has demonstrated this for *Uromyces caladii*. Apparently the host and parasite stand in a very perfect balance for a considerable time, especially in the case of rusts that are well adapted to the host. The host cells are not killed outright in such cases. In some of the rusts that are not well adapted to their host Stakman demonstrated that the host cells are killed immediately around the site of infection, thus isolating the parasite from the host tissues and causing its early death. The

death of the affected parts is mostly gradual. In some cases, e.g. the rusts of the small grains, the splitting of the epidermis by the numerous elongated sori of the rust seems to increase the water loss of the host plant to a very detrimental degree.

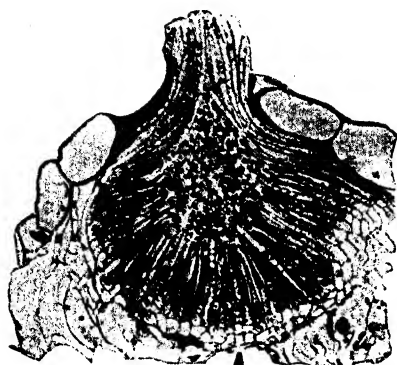
The promycelium of the Rusts is normally four celled, each cell having but one nucleus (Figure 84, F; 87, D, F; 89). It emerges through a thin spot in the teliospore wall, the germ pore. In shape the promycelium is variable depending upon the species. It may be long and slender, and nearly straight, each cell with a long sterigma, or short and thick and curved, constricted more or less at the septa. On such a curved promycelium the sporidia always arise on the convex side of the promycelium, usually on rather short sterigmata. In a number of genera the promycelium does not entirely emerge from the teliospore. Thus in *Zaghouania* the swelling of the teliospore bursts its thick wall allowing the emergence of a thin-walled, four-celled promycelium whose basal portion still remains enclosed within the old cell wall. In *Coleosporium* and *Gallowaya* (Figure 90, C) the teliospore divides by cross walls into four cells without emerging from the cell wall; thus producing a promycelium that is entirely internal. From each cell a long slender sterigma grows up through the gelatinous stratum that covers the tops of the layer of laterally adhering teliospores. In *Chrysopsora* each teliospore of the two forming the stalked compound teliospore segments internally (Figure 90, G) as in *Coleosporium*.

The uninucleate sporidia may be long ellipsoid, pointed or rounded at one or both ends, or may approach a spherical shape. The cell contents are usually somewhat yellow. The sporidium is shot off with more or less violence from the tip of the sterigma. Usually the whole contents of a promycelial cell pass into the single sporidium arising from that cell but occasionally a case is met with where the cell nucleus divides and one nucleus and part of the cytoplasm pass into the sporidium, so that a second sporidium may be produced from the same cell, as occurs more frequently in the Ustilaginales. A sporidium that fails to fall upon a suitable host is capable, under proper conditions of moisture, of producing a secondary sporidium at the tip of a sterigma and this in turn a tertiary or even quaternary sporidium, each being shot off from its sterigma. The successive sporidia are smaller and smaller. Under conditions of extreme humidity the author has observed the primary sporidia and the

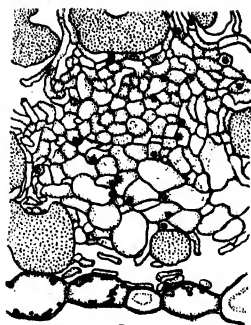
succeeding sporidia of *Kunkelia nitens* remaining attached in a short chain of four or five successively smaller cells.

When a sporidium falls upon the epidermis of a suitable host it germinates in a drop of rain or dew or film of water, forming a slender germ tube which, Dr. Ruth F. Allen shows, penetrates the cuticle and cell wall into the epidermal cell. The actual pore of entry is very small, the hypha on either side being several times as thick. Within the epidermal cell the hypha elongates and becomes divided into several uninucleate cells. From each of these a branch grows through the interior wall of the host cell either into an underlying cell, where it acts just as did the original infection hypha in the epidermal cell, or into an intercellular space where growth becomes much more rapid and the hypha becomes larger and more vigorous, and sends haustoria into the cells between which it passes. A few cases have been reported where entry took place through a stoma but these seem to be not usual. The infected area of the leaf often becomes thickened, in part at least through rapid formation of large amounts of rust mycelium, which forces the host cells apart and in some cases crushes them. The presence of the rust may cause marked changes in the manner of growth of the host. Thus in normally prostrate species of *Chamaesyce* (*Euphorbia*) the infected shoots become upright, a phenomenon also observed in other families of host plants. Abnormal growth of axillary buds in infected shoots gives rise to the witches' brooms so characteristic of some rust infections on Conifers. Dodge has shown that in leaves of *Rubus* infected by the orange rust (*Kunkelia nitens* and *Gymnoconia interstitialis*) the production of stomata which is usually confined to the lower epidermis of the host leaves is also brought about in the upper epidermis.

This monocaryon mycelium is of rather short duration in leaves and the stems of herbaceous plants. In woody plants it may persist for years, e.g. *Cronartium ribicola* in the tissues of the white pine (*Pinus strobus*) or *Gymnoconia interstitialis* and *Kunkelia nitens* in *Rubus* where the mycelium penetrates to the roots and infects the new shoots next year. From this monocaryon mycelium arise the spermatogonia (pycnia). These may be subcuticular or ^{of} epidermal (Figure 83, A) on leaves, green stems or fruit; ^{Office of} subcortical (Figure 82, B) on woody stems. Th ^{A, E, 1932;} basal pseudoparenchymatous mass of uninucle-



A



D



B



E



F



G



C



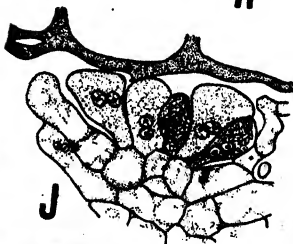
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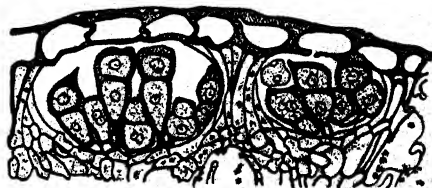


L



M

N



arise numerous parallel slender uninucleate sporophores. In these the nucleus divides and one of the two passes out into a terminal sperm cell (pynciospore) containing very little cytoplasm and surrounded by a thin cell wall. This is pushed loose by the formation of a second sperm cell below it and so on (Figure 82, *B*; 83, *B*). At the same time a sugary slime is secreted in which the sperm cells lie. The subepidermal spermatogonia may be more or less spherical structures (Figure 83, *A*) with a marginal series of paraphyses around the sporiferous portion. These push up through the epidermis rupturing it and producing an ostiole through which the sugary slime containing the sperm cells exudes as a shining drop sweet in taste. Sometimes the mass of spermatogonia is fragrant. The more diffuse subcuticular and subcortical spermatogonia also rupture the overlying cuticle or cortex, respectively, exposing the sugary exudate. Various insects particularly flies, attracted by the sweet liquid and accompanying fragrance visit the spermatogonia and feed on the exudate and go from leaf to leaf and plant to plant. In this way the sperm cells adhering to their feet or mouth parts become scattered widely over various plants and parts of the same plant. Rain, also doubtless helps in the dissemination of the sperms.

From the same monocaryon mycelium that has given rise to the spermatogonia and often near to these or on the opposite side of the leaf the hyphae begin to mass themselves, frequently at first in a substomatal chamber or other large intercellular space. Eventually this becomes a pseudoparenchymatous mass of cells, those nearer the surface being larger and less filled with food, the underlying cells being smaller and filled with food, the whole mass being more or less surrounded by several layers of hyphae. All the cells are normally uninucleate. This structure may be called an aecial primordium (Figure 83, *D*). In the dense portion of the pseudoparenchymatous tissue there begin to appear cells with two or more nuclei, whose origin will be discussed in the succeeding paragraphs. These cells elongate and may branch. At the apex toward the large pseudoparenchymatous cells binucleate aeciospores are budded off.

H and *I*, infection of leaf by urediniospores of *P. glumarum*; *J*, young telium of *P. glumarum*; *K*, *L*, *M*, stages in the development of the compound teliospore of *P. glumarum*; *N*, mature telia of *P. glumarum*. (After Miss Allen, Office of Cereal Investigations, U.S.D.A., in Jour. Agr. Res.; *B*, *C*, *D*, 1930; *A*, *E*, 1932; *F*, *G*, 1933; *H-N*, 1928.)

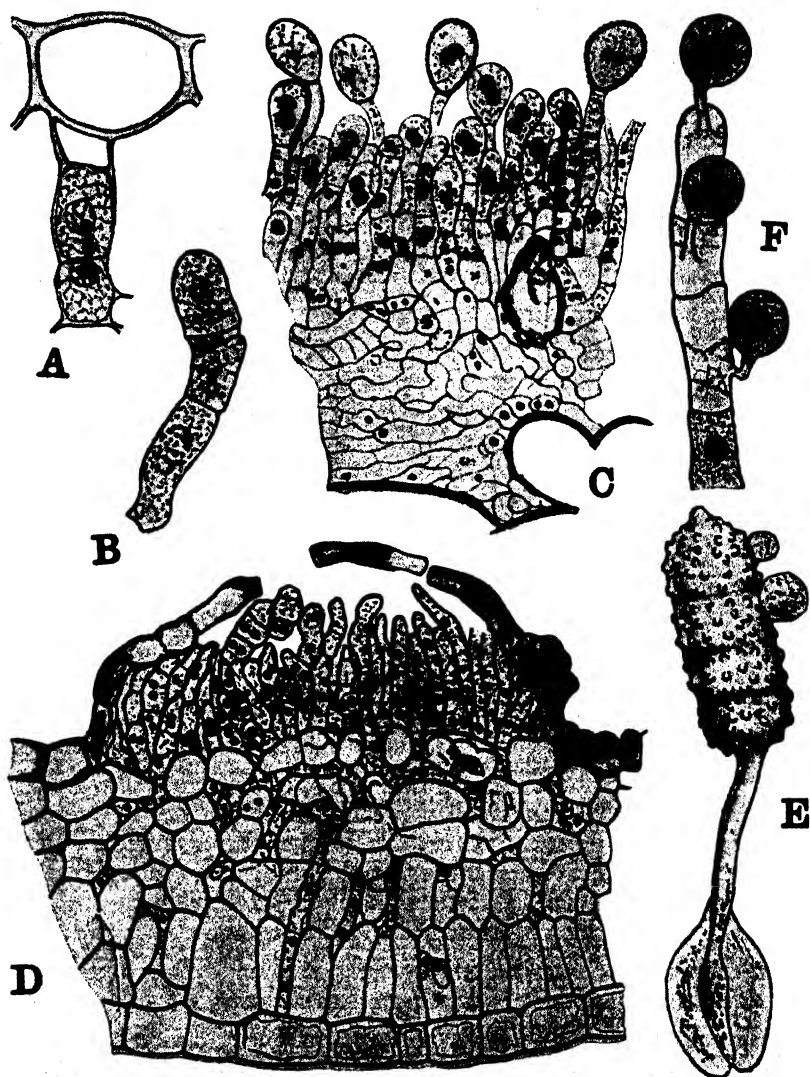


FIG. 84.—Uredinales. *Phragmidium violaceum*. A, origin of dicaryon basal cell for aecial chain; B, young aecial chain; C, portion of young uredinium; D, portion of young telium; E, compound teliospore, two cells beginning to germinate; F, promycelium, lowest cell not yet germinated. (After Blackman, 1904.)

After each spore is formed there is produced a smaller "disjunctor" cell, likewise binucleate, then another aeciospore, etc., until a chain of alternate spores and disjunctor cells results (Figure 82, *D*; 84, *B*). Between the original binucleate or plurinucleate cells others push their way in from the basal side of the aecial primordium and these also give rise to spore chains. In the mean time the large almost empty cells begin to collapse and digest, forming a space into which the chains of spores are pushed. Finally all of this tissue is crushed or destroyed. Around the sporogenous area a peridium may be produced or it may be wanting. The mass of spores eventually ruptures the overlying host tissues and the mass of spore chains and loose spores is exposed to the air (Figure 83, *C*). The spores are usually light to dark yellow or orange and somewhat roughened.

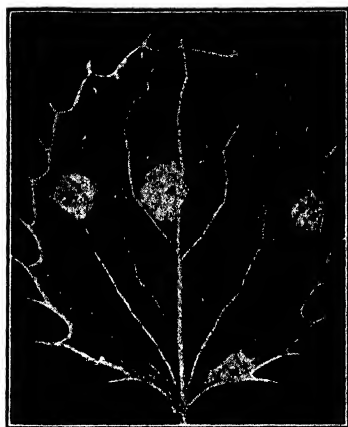


FIG. 85.—Uredinales. *Puccinia graminis*. Leaf of *Berberis vulgaris* with four monosporidial sori. To the two at the right was applied a mixture of spermatogonial exudations, thus leading to the formation of aecia. (After Craigie, 1931.)

Craigie demonstrated in 1927 that for *Puccinia graminis*, growing on barberry (*Berberis vulgaris*) and *P. helianthi* growing on sunflower (*Helianthus*) an infection with a single sporidium produces a sorus within which are produced numerous spermatogonia and aecial primordia. If this is protected from the visits of insects the latter never develop to spore production. However, if insects are allowed free access to this sorus and other sori as well, the aecia will develop within a few days. Furthermore, by transferring the sperm cells from one sorus to the surface of another in half the cases aecia develop (Figure 85). Craigie finally demonstrated that the four sporidia were of two sexual phases, two sporidia of each phase, and that sperm cells from the sorus of one sexual phase, would fertilize the sorus of the other sexual phase, and vice versa. In later papers he has added *P. coronata*, *P. pringsheimiana* and *Gymnosporangium* sp. to the list. Andrus has confirmed this for *Uromyces appendiculatus* and *U. vignae* and Miss Allen for *Puccinia*

trititina and several other species of Rusts. Indeed it seems probable that all Rusts producing spermagonia have these two sexual phases. If two sori from sporidia of opposite sexual phases lie close together aecia will develop where they come into contact without the help of the sperm cells. Brown has shown that a dicaryon mycelium (e.g. uredinial sorus) can also induce aecial formation in a sorus from a sporidial infection. Hanna found that 48 hours after a mixture of sperm cells of opposite sexual phases was applied to a sorus of *Puccinia graminis* on the leaf of barberry the cells at the base of the aecial primordium became binucleate. Using mixtures of sperm cells from different physiological forms of *Puccinia graminis* on wheat, Waterhouse in Australia obtained two hitherto unknown forms which are probably to be interpreted as crosses between the original strains. Similar experiments by Newton and others in Canada and by Stakman and others in Minnesota resulted not only in interracial crosses but in crosses between *P. graminis tritici* and *P. graminis secalis* and between the former and *P. graminis agrostidis*. In the course of the various crosses several new physiological forms have been produced. The results of the crosses reveal that many of these forms must be heterozygous. This was further demonstrated by the production of selfed strains. Thus physiologic form #17 when selfed (i.e. fertilized by sperm cells of the same form but opposite sexual phase) produced aeciospores which gave rise to the same strain and seven others besides and form #53 gave besides itself seventeen other forms. On the other hand form #9 proved to be homozygous.

Andrus demonstrated for the two species of *Uromyces* mentioned above that there are certain elongated filaments, which he calls "trichogynes," whose tips emerge from the stomata or between epidermal cells and to which the sperm cells adhere. The nucleus of the sperm enters the trichogyne and passes down through it. Only then do the multinucleate cells appear in the aecial primordium. Miss Allen has demonstrated the occurrence of similar receptive hyphae (Figure 83, E) in *Puccinia trititina* and other species of Rusts (Figure 83, F, G) and J. L. Forsberg (in an unpublished thesis) has shown their presence in *Kunkelia nitens* and *Gymnoconia interstitialis*. Miss Rice has shown that similar structures are formed in a number of other rusts. According to Andrus these "trichogynes" are filaments running out from certain uninucleate cells

("egg cells") in the basal portion of the aecial primordium. The sperm nucleus after its entry follows down through the trichogyne, the septa dissolving as it approaches, until it reaches the "egg cell" into which it passes (Figure 86, *B*). There the two nuclei divide and the first spore is formed (Figure 86, *A*). The egg cell may branch so as to give rise to several chains of spores. According to Miss Allen the receptive cells, into which the one or more (up to

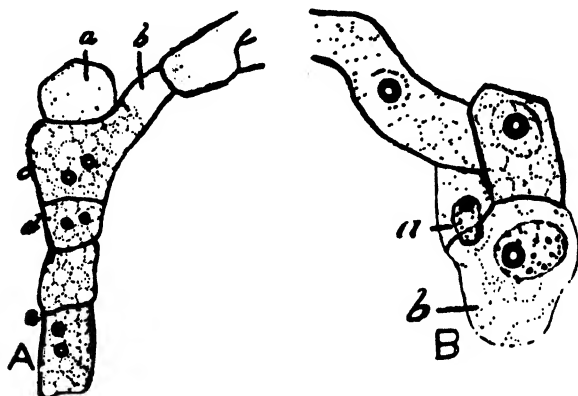


FIG. 86.—Uredinales. Sexual reproduction in *Uromyces*. *A*, fertilized basal cell (*c*) with stalk cell (*a*) and trichogyne (*b*); *B*, male nucleus (*a*) entering egg cell (*b*). (After Andrus, in Jour. Agr. Res., 1931.)

10 or so) sperm nuclei pass, elongate and branch and form a dicaryon mycelium which penetrates into the basal portion of the aecial primordium where the dicaryon (or plurinucleate) cells give rise to the chains of spores. In a later paper Miss Allen shows that in *Puccinia sorghi*, whose aecial stages are produced in species of *Oxalis*, the paraphyses extending from the ostiole of the spermatogonium are receptive hyphae (Figure 83, *F*, *G*) as was shown for *P. helianthi* by Craigie. The union of sperms to these paraphyses was shown and the actual passage of the sperm nucleus into the paraphysis. In her work on *P. triticea* and more particularly on *P. graminis* she shows that receptive hyphae may emerge from stomatal openings or between epidermal cells, in addition to the spermatogonial paraphyses which serve as receptive hyphae. Rather than the growth of new sporophytic hyphae to the aecial primordium it may be that a process of diploidization occurs as described by Lehfeldt and by Buller for the Basidiomyceteae. This consists

of the division of the nuclei of the introduced sexual strain and their passage through the septa from cell to cell of the mycelium until it now is completely "diploidized" i.e. each cell possesses nuclei of both sexual strains.

In addition to the processes described above Blackman, Christman, Mme. Moreau, Colley and many others have described another manner by which the aeciosporic chains are originated. A layer of uninucleate cells in the basal portion of the aecial primordium either shows fusions by twos, the walls between the upper portions of these cells dissolving out (Figure 82, C), resulting in a binucleate two-legged cell, or nuclei pass from adjacent cells through small pores (Figure 84, A) to form a dicaryon cell. From this, by conjugate division of the nuclei and the formation of successive cells comes a chain of aeciospores and intercalary (disjuncter) cells (Figure 82, D; 84, B). Just how the two sets of uniting cells originated was not made clear by these authors, but the very recent observations of Miss Allen on *Melampsora lini* suggest how it may have occurred in the species investigated by them. In this rust, which like *Puccinia helianthi* occurs in two sexual strains, the germ tubes from the sperm cells enter the epidermis of a sorus or penetrate through a spermagonium and form in the host tissues a mycelium whose hyphae pair with the hyphae of the aecial primordium to produce a layer of basal two-legged cells from which arise the chains of aeciospores. In 1888 Massee reported the occurrence of oogones and antherids in the aecial primordium. From below the oogone he reported the outgrowth of hyphae which formed the protective envelope of the aecium while from the oogone itself budded out hyphae which became the chains of aeciospores. In the light of the observations of Craigie, Andrus and Miss Allen it is clear that Massee misinterpreted certain structures that he saw and illustrated.

From the foregoing accounts it is clear that in some and probably all Rusts the sperm cells are functional. Furthermore, the same haploid mycelium produces both sperm cells and receptive hyphae (trichogynes) so that both male and female structures are present, yet self fertilization does not occur. Like the condition in *Pleurage anserina* reported by Ames, in *Neurospora* as demonstrated by Shear and Dodge and in *Sclerotinia gladioli* studied by Drayton, two

sexual phases are present, each hermaphroditic but incapable of self fertilization.

The binucleate aeciospores are capable of remaining viable for a long time and can be carried long distances by the wind and then cause infection. Falling upon a suitable host plant the spore germinates in a drop of water (dew, rain, etc.) forming a stout germ tube which seeks out and enters a stoma, never penetrating the epidermis directly as do the germ tubes from the sporidia. Just within the stomatal opening the hypha enlarges to form a "sub-stomatal vesicle" containing many nuclei from which arise hyphae of dicaryon cells which penetrate the host tissue in various directions, growing intercellularly and sending haustoria into some of the cells between which they pass. Usually the size of the infected area from one aeciosporic infection is limited, i.e. the fungus in this phase is not capable of indefinite growth. When its full extent of development is nearly attained a subepidermal mass of hyphae is formed making a pseudoparenchymatous basal layer (like the mycelium, of dicaryon cells) from which grow short upright two-celled branches. These raise and eventually rupture the epidermis, thus producing a uredinial sorus (uredinium, Figure 82, *E*; 84, *C*). The outermost of the two cells enlarges to form a binucleate urediniospore while the other elongates to form its long stalk. The urediniospores are usually yellow to orange-red in color, mostly finely verrucose or echinulate. There are several germ pores for each urediniospore and their number and position on the spore are of great assistance in the identification of the various species. They break loose from the stalk and like the aeciospores may be carried long distances by the wind. They germinate and infect the host through the stomata in exactly the same manner as do the aeciospores (Figure 83, *H*, *I*). As long as the host plant has not passed a certain stage of growth these new infections produce other crops of urediniospores. As the host plant becomes more mature teliospores begin to appear, often at first intermingled with the urediniospores in the same sorus, but eventually in sori containing only teliospores. They arise from the same type of pseudoparenchymatous subepidermal mycelium as do the urediniospores. From this basal layer there grow upward series of dicaryon cells (Figure 82, *F*; 83, *J*; 84, *D*). Some of these may differentiate into stalk cells and teliospores or all may become teliospores. In some

of the most primitive rusts no basal layer is formed and the teliospores are produced singly or by twos or threes as enlarged cells of the mycelium in the interior of the leaf. The young teliospores, whatever their shape or location are at first binucleate. The two nuclei unite to form a diploid nucleus (Figure 83, *J-M*; 84, *D*). Usually the teliospore becomes thick-walled (mostly with one or more germ pores) and more or less colored (from light yellow-brown to almost black).

From the mature, uninucleate teliospore the promycelium emerges at once (various species of *Cronartium*, Figure 82, *F*, *Puccinia malvacearum*, etc.) or only after over-wintering (*Puccinia graminis*) or after certain unfavorable environmental conditions have passed. It emerges through one of the germ pores and into it may pass the undivided nucleus of the teliospore or the first of the two divisions of the nucleus may occur before the nuclei enter the promycelium. The final division usually takes place in the promycelium whereupon septa are formed dividing it into four cells. Sometimes a further septum cuts off the teliospore from the basal cell of the promycelium. From the promycelial cells the sporidia are formed and shot off from the sterigmata.

Rusts may be either autoecious or heteroecious. In the former the sporidial and aeciosporic infections take place on the same or closely related species of host while in a heteroecious species the host infected by the sporidia belongs to a family not at all closely related to that containing the host for the aeciosporic infection. Heteroecism was first proved by actual inoculation experiments by de Bary in 1865 for *Puccinia graminis* and by Oersted for *Gymnosporangium sabinae* in the same year. The former showed that the aeciospores produced on the common barberry (*Berberis vulgaris*) would not infect that species but would infect the small grains; wheat, barley, etc. The urediniospores would infect the same and often also closely related species of hosts. The sporidia from the teliospores on the overwintered straw or stubble would, on the contrary, infect only the barberry. Thus was brought the scientific explanation of a phenomenon known for a hundred years or more that the presence of barberry plants was detrimental to small grains. This much had been definitely proved by careful observation and experiment long before but the actual connection of the rust on barberry to that on the grain was left for de Bary to prove. Since that time the

heteroecism of hundreds of species has been demonstrated. It is worthy of note that Waterhouse has discovered one physiological form of wheat rust that is incapable of infecting barberry.

In an autoecious species the aeciospores infect the same or closely related host species as did the sporidia. Thus *Puccinia helianthi*, the rust of the sunflower (*Helianthus annuus* and other species) has its sporidial infection on the sunflower with the production of the monocaryon mycelium which produces the spermagonia and the aecial primordia. Infection by aeciospores produces in the same host species, even in the same plant, the dicaryon mycelium from which arise the urediniospores and teliospores. It may happen that both types of infection may occur on the same leaf.

Of the rusts of more or less economic importance the hosts are indicated below for the different stages of a few species, showing that both heteroecious and autoecious rusts may be enemies of cultivated plants. The list contains a very few of the many rusts that attack plants of economic importance. The customary symbols are used, viz. 'O' = spermagonial development, I = aecial stage, II = uredinial stage, III = telial stage.

Heteroecious Species.—*Puccinia graminis*, black stem rust of small grains, O and I on *Berberis vulgaris*, barberry, II and III on small grains (wheat, rye, barley, oats) and various other grasses.

P. triticina, leaf rust of wheat, O and I on species of *Thalictrum*, II and III on wheat (*Triticum*).

P. coronata, crown rust of oats, O and I on various species of *Rhamnus*, II and III on oats (*Avena sativa*).

P. sorghi, O and I on *Oxalis stricta*, II and III on maize (*Zea mays*).

Gymnosporangium juniperi-virginianae, O and I on apple (*Malus malus*), III on red cedar (*Juniperus virginiana*).

Uromyces carophyllinus, O and I on *Tithymalus* sp., II and III on carnation (*Dianthus caryophyllinus*).

Cronartium ribicola, White Pine Blister Rust, O and I on White Pine (*Pinus strobus*), II and III on various species of currant (*Ribes*) and gooseberry (*Grossularia*).

Uredinopsis spp., O and I on species of fir (*Abies*), II and III on various ferns.

Autoecious Species.—*Gymnoconia interstitialis*, O, I and III on blackberry, dewberry and black raspberry (*Rubus* spp.).

Uromyces appendiculatus, O, I, II and III on American beans (*Phaseolus vulgaris*).

Puccinia asparagi, O, I, II and III on asparagus (*Asparagus officinalis*).

P. helianthi, O, I, II and III on sunflower (*Helianthus annuus* and some other species).

P. malvacearum, III (only stage produced) on hollyhock (*Althaea rosea*) and other Malvaceae.

Phragmidium spp., O, I, II and III on various species of rose (*Rosa* sp.).

In the case of heteroecious rusts efficient control can be obtained by the elimination of the alternate host where the rust is unable to overwinter on the host that is of economic importance. Thus in the northern portions of the United States and of Europe the extermination of the barberry has greatly reduced the ravages of the black stem rust (*Puccinia graminis*) because this rust can not survive the winter on the overwintering wheat or rye or other grains. In the southern portions of the United States and Europe the rust is not killed out by the winter cold and so perpetuates itself by its urediniospores. Under such conditions the eradication of the barberry has little effect. The apple rust (*Gymnosporangium juniperi-virginianae*) has been found to be susceptible to control by removal of its alternate host, the red cedar (*Juniperus virginiana*) over an area to a distance of a mile or more from the orchard that is to be protected. White Pine Blister Rust (*Cronartium ribicola*) requires the destruction of all *Ribes* and *Grossularia* plants to a distance of half a mile (one mile for *Ribes nigrum*) from the trees it is desired to protect. *Puccinia triticina*, although heteroecious, can not be controlled in this manner for the rust that infects the wheat in the Fall survives the Winter on this host and produces urediniospores in the Spring from which the disease is spread. In fact this rust is exceedingly abundant in many parts of the United States where the host for the aecial stage does not occur.

The rust life cycle described in the foregoing pages is the typical cycle. Rusts possessing such a cycle are called macrocyclic or long-cycle rusts. Arthur, Orton, Jackson and others believe these to represent the more primitive life cycle so far as present rusts are known. Many species of rusts have shortened their life cycle by the omission of one or more stages. Dietel, Olive and Grove con-

sider these to be the more primitive. Thus most species of *Gymnosporangium* produce no binucleate repeating spores (urediniospores) from the dicaryon phase of growth. Some rusts produce only spermagonia and telia while still others omit the spermagonia also (e.g. *Puccinia malvacearum*). These last two are properly speaking microcyclic rusts. There are also rusts in which no true telia are produced but whose aeciospores germinate in the manner

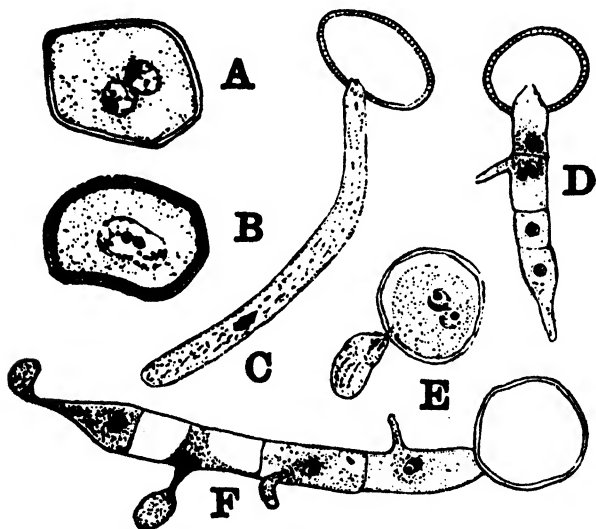


FIG. 87.—Uredinales. A-D, *Endophyllum sempervivi*. A, binucleate aeciospore; B, aeciospore with nuclei united; C, germinating aeciospore; D, promycelium formed; E-F, *E. euphorbiae-sylvaticae*. E, aeciospore germinating without union of nuclei; F, promycelium and sporidia. (After Moreau and Moreau, 1919.)

of teliospores by the formation of a promycelium. These rusts also are microcyclic. *Kunkelia nitens* on *Rubus* spp. is of this type as are the various species of *Endophyllum* (Figure 87). The microcyclic species are of especial interest as regards the origin of the binucleate condition of the young teliospore. In one of these microcyclic species (*Puccinia arenariae*) Lindfors describes the formation of a two-celled promycelium, each cell giving rise to a binucleate sporidium. This produces a dicaryon mycelium and no monocaryon mycelium occurs at all. Possibly similar conditions may be found in other microcyclic forms that lack spermagonia. Miss Allen has found that in *Puccinia malvacearum* the teliospores

arise from dicaryon mycelium. The two nuclei unite and then divide in the promycelium in the usual way. The nucleus undergoes division in the sporidium, but Miss Ashworth finds that it gives rise to a monocaryon mycelium. According to her investigations certain cells in the telial sorus show nuclear migrations producing the dicaryon phase. However, in those rusts where spermagonia and telia (or aecia whose aeciospores germinate with promycelium) occur it has been shown that the mycelium is of a monocaryon type until the telium (or aecium) is formed, when dicaryon cells appear. It is probable that this dicaryon phase arises in the same way as described above for a macrocyclic rust. The transfer of the production of the promycelium back from the teliospore to the aeciospore has apparently taken place independently several times so that the microcyclic rusts of the formula *O, I* are not necessarily closely related but have probably developed independently from *O, I, (II) III* forms. It is clear that *Kunkelia nitens*, the microcyclic orange rust of *Rubus*, is derived from *Gymnoconia interstitialis* a long cycle form (*O, I, III*) on the same hosts. The genus *Endophyllum* represents a similar series of cases. Some of the species of this genus correspond in aecial host and structure to the aecial stage of known macrocyclic species. These abbreviated forms may lack the fusions of the two nuclei within the spore before the formation of the promycelium. Thus Dodge has shown that in *Kunkelia nitens* the two nuclei pass out into the promycelium, each dividing again to form the four nuclei which pass out into the sporidia. The Moreaus have found the same to be true for *Endophyllum euphorbiae-silvaticae* (Figure 87, *E, F*), but in other species of the genus have demonstrated nuclear fusion (Figure 87, *A-D*) in the aeciospore before the promycelium is formed. In one form of *Kunkelia nitens* Dodge has shown that no dicaryon cells are produced and the aeciospores also are uninucleate and produce a two-celled promycelium.

A third type of life cycle is that usually designated as *O, II, III*, i.e. a cycle in which the typical aecial structure is lacking. The spermagonia are succeeded by sori containing spores exactly resembling typical urediniospores. In the same way as are produced the dicaryon basal cells of the chains of aeciospores Christman has shown that there are produced dicaryon cells giving rise to urediniospores. The latter give rise to dicaryon mycelium from which may arise later another series of urediniospores. The usual interpretation

of this phenomenon is that this is really a macrocyclic rust of the formula *O, I, II, III* in which the aeciospores are not produced in chains but singly on stalks, like urediniospores. The primary (first produced) urediniospores are therefore modified aeciospores and the secondary urediniospores are true urediniospores.

The aecium may be cup-shaped (cupulate) with a well developed peridium (Figure 83, C) or this may be very tall so as to make a horn-like (cornute) structure. The peridium may be lacking so

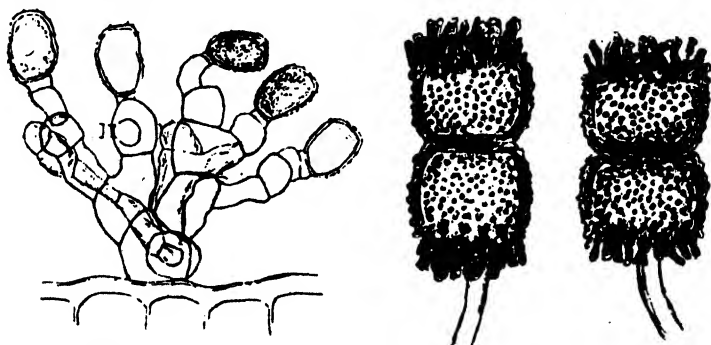


FIG. 88.—Uredinales. *Dasyscypha foveolata*. Two compound teliospores and branched external aecium. (After Sydow, 1925.)

that the aecium is diffuse. Other forms are known, the most curious of which is the hyphoid aecium of *Dasyscypha foveolata* in which a branching dicaryon mycelium emerges through various stomatal openings, forming a colorless mass of hyphae (Figure 88). These are terminated by single (not catenulate) aeciospores which drop off while the hypha elongates sympodially and produces another aeciospore, and so on.

The uredinium may be merely a cluster of stalked urediniospores bursting through the epidermis of the host or it may be surrounded by paraphyses. In *Pucciniastrum* and closely related genera the uredinia possesses a true peridium (Figure 82, E). In some genera e.g. *Coleosporium* the urediniospores, like the aeciospores, are produced in chains but they arise from a dicaryon mycelium and so differ from aecia.

The telium is the most variable. Properly speaking a teliospore is a single cell, binucleate at first but becoming uninucleate by the fusion of the two nuclei; and giving rise immediately or later to a promycelium. The teliospores are produced under the epidermis

or in the mesophyll or very rarely (*Cystopsora*, *Goplana*) the basal cells from which they arise may push out through a stoma so that the teliospores are then produced externally. The stalked types of teliospores are formed subepidermally and become external by the rupture of the epidermis. In some genera the teliospores are formed

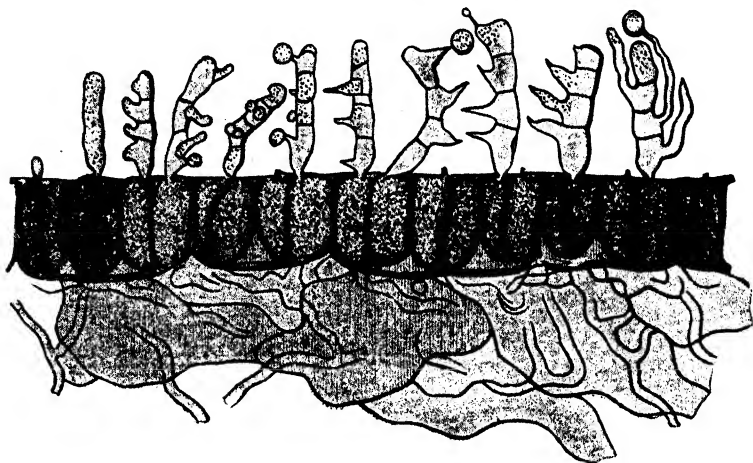


FIG. 89.—Uredinales. *Calyptospora goeppertiana*. (After Hartig, 1889.)

in separable chains and the telium is surrounded by a peridium which bursts the epidermis and opens to allow the teliospores to escape. In the fern rusts of the genus *Uredinopsis* the teliospores are produced in the mesophyll of the leaf, singly or united two, three or four together into a compound teliospore, each of whose component cells gives rise to a separate promycelium which emerges from the leaf surface. In *Calyptospora* (Figure 89) the teliospores are produced in groups of two to four cells in the epidermal cells of the host. In *Pucciniastrum* (Figure 90, A) the clusters of two to four teliospores are aggregated laterally into a subepidermal crust. In *Cronartium* (Figure 82, F) the teliospores are joined laterally and longitudinally into a tall waxy column which pushes out through the epidermis to a length of up to 6 or 8 mm. In *Melampsora* (Figure 90, B) and *Coleosporium* the teliospores are crowded laterally into a subepidermal or subcuticular crust. Among the stalked forms *Uromyces* has but a single teliospore at the apex of its stalk, *Puccinia* has two united teliospores on the single stalk

(Figure 83, *N*), in *Phragmidium* one stalk bears a row of 3 to 8 or more teliospores. In *Puccinosira* the telium has a peridium and the teliospores are formed on a stalk in chains which break apart into units of two united teliospores, each. In *Ravenelia* (Figure 90, *F*) the stalk bears a head of laterally united teliospores below which are colorless cells, the so-called "cysts." Usually in systematic literature these various types of compound teliospores are spoken of as single teliospores although properly each cell from which a promycelium arises is a teliospore.

The order has been divided into many families or into two families. The author follows Dietel and the later works of Arthur, both of whom recognize but two families each divided into several tribes.

FAMILY MELAMPSORACEAE.—Teliospores without stalks, produced singly or united in groups of 2 to 4 in the mesophyll or just below the epidermis, or united laterally into subepidermal or subcuticular crusts, or united into vertical chains which may be separate or united laterally into a waxy column which bursts through the epidermis. Aecia mostly on species of Family Pinaceae. 15 to 20 genera and about 300 species. This family clearly includes the more primitive representatives of the order. The genus *Uredinopsis* with its colorless teliospores, single or united by 2's, 3's or 4's, in the mesophyll of the leaves of Ferns, its two kinds of colorless urediniospores, thin walled and thick walled, the sori surrounded by peridia, and with its aecia and spermagonia on the needles of species of *Abies* probably combines the greatest number of primitive characters of any rust, viz. telial hosts in the ancient group Pteridophyta, colorless urediniospores and teliospores, the latter scattered in the mesophyll, uredinia surrounded by peridium, etc. Two other genera (*Hyalospora* and *Milesina*) with colorless teliospores formed in the epidermis cells are also found in the Ferns. *Calyptospora* (Figure 89) is of interest because it is one of the few rusts in which the sporophytic (dicaryon) mycelium is perennial. The aecia occur on the leaves of the fir (*Abies*) as is true of the other genera already mentioned. The telial stage (no uredinia are known) occurs in *Vaccinium*, its presence causing the development of a sort of witches' broom with upright thickened stems and small distant leaves. The mycelium grows out into the epidermal cells of the stem, there forming clusters of 2 to 4 closely united teliospores which send forth their promycelium almost immediately; through

the epidermal cell walls. In *Cronartium* the gametophytic (monocaryon) mycelium is perennial in the twigs and cortex of older limbs of pine (*Pinus*), often causing the formation of galls which may attain great size and age, up to the size of a human head in *C. cerebrum*. The uredinia are small with a peridium (Figure 82, E). The telia are rows of teliospores united laterally into a waxy column six to eight rows in thickness and bursting through the epidermis

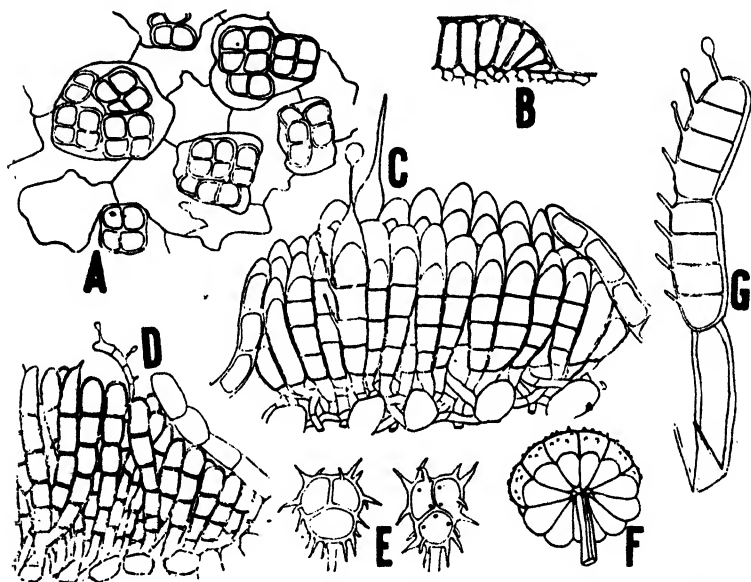


FIG. 90.—Uredinales. Teliospores. A, *Pucciniastrum circueae*; B, *Melamp-sora ribesii-viminalis*; C, *Gallowaya pini*; D, *Chrysomyxa rhododendri*; E, *Triphrag-mium echinatum*; F, *Ravenelia acaciae-micranthae*; G, *Chrysopsora gynoxidis*. (After P. and H. Sydow, 1915.)

(Figure 82, F) and projecting several millimeters (up to 6 or 8 in *C. cerebrum* collected by the author on *Quercus borealis*), continuing to grow at the base for some time. Each of the hundreds of teliospores of the column germinates immediately by a curved promycelium producing almost spherical sporidia. The dicaryon stage is found in various Flowering Plants (Anthophyta), apparently only in Dicotyledoneae. In *Chrysomyxa* (Figure 90, D) the teliospores are in separate chains of three or more spores which arise at the base of the sorus. The urediniospores are also in chains. The sporophytic phase occurs in the Family Ericaceae in the wider

sense. *Coleosporium* and *Melampsora* (Figure 90, B) both produce subcuticular or subepidermal crusts one cell thick of laterally united teliospores. In the former the urediniospores are produced in short chains and the promycelium is "internal," in the latter the urediniospores are single and the promycelium is typical in structure. *Coleosporium solidaginis*, on *Aster* spp. and *Solidago* spp. is abundant even in those parts of the United States where the aecial hosts (species of *Pinus*) are not found. It is apparently able to maintain itself by overwintering urediniospores. *Melampsora* species cause the spotting of leaves of various species of poplars (*Populus*) with the dark colored telial sori, these being preceded by the small powdery yellow uredinial sori. The aecial host is the larch (*Larix* sp.) on whose young needles the almost white aecia appear.

FAMILY PUCCINIACEAE.—Teliospores usually stalked, simple or compound, sometimes without stalks and produced successively as simple or compound teliospores which escape from the sorus dry or embedded in slime. Aecia only very exceptionally on Pinaceae. The stalked forms of this family are easily distinguished from the Melampsoraceae but the forms with teliospores produced in loose, quickly fragmenting chains are a sort of connecting group difficult to segregate definitely from one or the other family. Dietel recognizes 83 genera and about 3000 species while some authors add at least 20 genera by the segregation of the larger genera such as *Uromyces* and *Puccinia*. These two are among the more important genera of the family with, respectively, about 600 and over 1800 species. The spermagonia are subepidermal, the aecia are cupulate and the uredinia are without peridium, with urediniospores single on long stalks, in both genera. The teliospores are brown and stalked, emerging from the ruptured epidermis. In *Uromyces* they are simple, in *Puccinia* compound, formed of two teliospores closely united in a row with a one-celled stalk (Figure 83, N). A number of cases are known where the aecia of heteroecious species of the two genera are borne on the same host and the urediniospores and teliospores on the same alternate host, the aeciospores and urediniospores of the respective species of *Uromyces* and *Puccinia* being practically indistinguishable. The only essential difference is that in the one genus the pedicel is topped by a single teliospore and in the other by two. Arthur believes that the frequency of such cases indicates a very close relationship of the two genera. In

Phragmidium (Figure 84, *E*) the row of teliospores is longer, 3 to 8 or more in a row, and the stalk is long and enlarged toward the base. In *Gymnosporangium* (with 40 or more species) the stalks are very long and their walls as well as the outer walls of the two-celled compound teliospore swell when wet so that the masses of teliospores are extruded from the telial galls as gelatinous tongues sometimes 2 to 3 cm. in length. The aecial hosts of this genus with few exceptions belong to the Malaceae and the telial hosts are species of *Juniperus* or closely allied genera. This genus forms rather an exception in that it is the dicaryon stage that is perennial, the galls on the host persisting sometimes for several years. *Ravenelia* and *Haploravenelia* are genera whose teliospores form a head of one layer of fertile spores subtended by colorless "cysts" which probably represent sterile teliospores (Figure 90, *F*). This head is supported by a centrally attached stalk usually several cells in thickness. These genera are mostly tropical and subtropical and are autoecious so far as known. *Gymnoconia* resembles *Puccinia* in its two-celled, compound teliospore but the aecia are diffuse, without peridium, and the spermagonia are subcuticular. Urediniospores are lacking.

In addition to the genera and species assigned to these two families there are over 1000 species of which the telial stage is unknown or not connected with the other stages. *Peridermium*, *Aecidium* (600 species) and *Caeoma* represent different types of aecia. *Uredo* (450 species) consists of species of which the uredinial stage only is known. In most of these cases there are probably other stages as yet unknown or whose connection with these has not yet been demonstrated but it is possible that in some of these species the other stages have been omitted during the course of evolution.

Order Ustilaginales.—The Smuts are parasitic, but capable of growth as saprophytes on substrata rich in organic material, e.g. well manured fields. Flerov and also Sartoris have grown several species of *Ustilago* from teliospore to teliospore on artificial culture media apart from their hosts. In the host plant the mycelium is intercellular, with or without haustoria, and actively growing in and keeping pace in its growth with that of the meristematic regions of the host plant, usually dying in the parts of the host that have passed the meristematic stage. Seyfert investigating several

species in Europe and Stakman and Christensen studying *Ustilago zaeae* and Hanna investigating the same species seem to have demonstrated that clamp connections are often present in the dicaryon phase of growth (Figure 91), but Sleumer claims that these are not true clamp connections but abortive branches. The nuclear behavior as reported by Seyfert would support the idea that they are typical clamp connections. The teliospores are produced largely in the flowers, fruits and inflorescences, but in many cases are produced in the leaves or stems. More often the masses of telio-

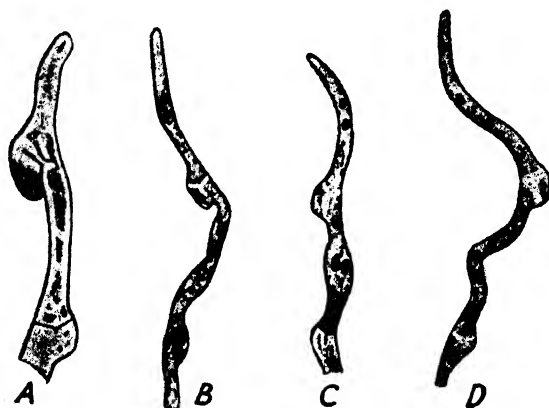


FIG. 91.—Ustilaginales. Clamp connections in mycelium of *Ustilago vaujckii*. (After Seyfert, 1927.)

spores are dusty at maturity, and with the rupture of the host tissues are set free for distribution by the wind or other means. The sporidia are shot from the promycelium with considerable force in the Family Tilletiaceae. Conidia are mostly produced on the saprophytic mycelium but in *Tubercinia* (Figure 93, D) and *Entyloma* are produced abundantly on the surface of the living leaves of the host plant on long conidiophores which emerge from the epidermis and give a whitish appearance to the affected leaf. When a conidium arises from a cell of monocaryon mycelium the nucleus of the cell divides and one of the daughter nuclei passes out into the conidium which grows out from one side of the hyphal cell. If the cells are binucleate both nuclei divide simultaneously and one daughter nucleus of each pair passes out into the developing conidium, or but one nucleus enters the conidium.

Infection of the host plant takes place only in meristematic tissues, by means of sporidia or conidia or by a germ tube produced in place of the sporidia. The Smuts fall roughly into three groups with reference to the manner of infection: (1) Infection takes place as the seed germinates, either from sporidia (or germ tubes) produced on promycelia from teliospores adhering to the seed or from sporidia or conidia present in the soil. This type of infection can be controlled by treating the seeds with suitable disinfectants before planting in soil free from the smut. Examples are *Ustilago avenae*, oat smut, *Tilletia levis* and *T. tritici*, both of which cause stinking smut or bunt of wheat, *Urocystis occulta*, causing stem smut of rye and many other smuts. (2) Any actively growing meristem may be infected by sporidia or by conidia. In the case of maize smut, *Ustilago zeae*, the infection may occur on young roots, at any joint of the stem (i.e. the meristem at the base of each internode), on young, not yet unrolled leaves, on the male inflorescence (tassel) before it emerges, on the young ear or certain grains of the ear, and even on the elongated styles ("silks") on which N. F. Petersen¹ has shown that it may cause small galls. Treatment of the grain with disinfectants is of little value in controlling this type of infection. Planting must be done in soil free from the fungus. (3) Infection of the flower at times of blooming. This was worked out by Brefeld. It occurs in the loose smuts of wheat and barley, *Ustilago tritici* and *U. nuda* respectively. When the host plant has headed out the flowers are normally self-pollinated before opening. When they open the teliospores from nearby diseased plants germinate and produce their sporidia (or germ tubes) on the stigmas and infect them, passing down into the ovary and entering the developing embryo, in the growing point of whose stem the mycelium becomes dormant until the grain is planted. Then it grows actively in the apical meristem, causing little apparent injury to the host plant until the head is being produced. Within this developing head the mycelium grows very vigorously reducing it to a skeleton surrounded by the powdery masses of spores which are set free at just the time the healthy plants are coming into flower. Control is possible by soaking the infected grain in water and then dipping into hot water at a temperature and for a length of time that will kill the contained mycelium without killing the grain.

¹ In a letter to the author.

Smuts may cause large galls consisting in part of host tissues and in part of fungus tissues. These galls of maize smut (*Ustilago zeae*) may attain a large size and are edible when young. Various leaf smuts cause the production of galls, e.g. *Doassansia* on the leaves of species of *Sagittaria*. Many smuts, on the other hand, do not show their presence until their teliospores are formed. In the case of *Ustilago violacea* attacking several species of *Dianthaceae* the teliospores are formed only in the anthers. When the female plant of a dioecious species of *Lychnis* is infected the presence of the fungus causes the flower to produce stamens, within which the fungus produces its spores although the normal female flower lacks stamens.

The order is divided into two families:

FAMILY USTILAGINACEAE.—Promycelium transversely septate into several, mostly four cells (Figure 92, A-G). The teliospores arise from transformed dicaryon cells of the mycelium. The cell walls of the usually tangled hyphae swell and undergo gelatinization, thus separating the

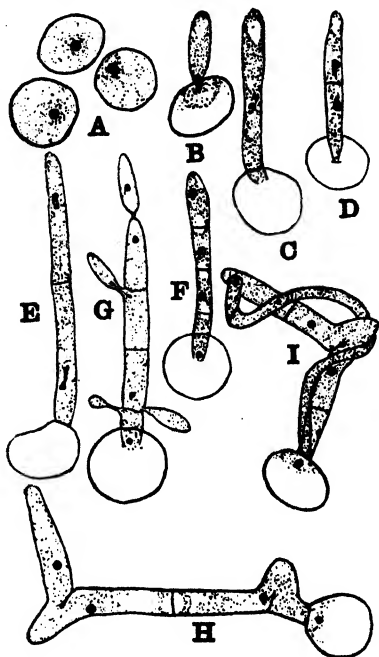


FIG. 92.—Ustilaginales. Types of germination of *Ustilago hordei*. A-G, normal development of promycelium and sporidia; H and I, types of conjugation between promycelial cells of opposite sexual phase. (After Hüttig, 1931.)

protoplasts to some distance. Around these then, within the gelatinized walls, new walls are laid down and the cells enlarge while the gelatinized walls disappear. At about the same time the two nuclei unite and the teliospores come to maturity. The teliospores are produced singly or united into spore balls. They are usually dark colored, with wall more or less thickened and smooth or rough. From each cell of the promycelium usually several sporidia are produced, for, unlike the majority of Uredinales, the nucleus of the cell divides several times and one of the daughter

nuclei enters each sporidium. In some cases each promycelial cell grows out into a slender germ tube instead of producing sporidia. This difference in behavior is connected for some species with differences in temperature, moisture, etc. In *Ustilago nuda* and *U. tritici* sporidia are apparently never formed.

Sexual reproduction in this family is accomplished in various ways. In several species it has been determined that two of the promycelial cells represent one sexual phase and the remaining two the other phase. The distribution of the two sexual phases in the four cells of the promycelium may apparently occur in every possible order. In *Ustilago zeae* Hanna has shown that there occur four sexual phases. Apparently there are two allelomorphic pairs of genes on separate chromosome pairs that control this sexual behavior. If both chromosome pairs undergo their reduction (disjunction) division in the first or in the second of the two divisions occurring in the production of the promycelium two of the promycelial cells will be of one sexual phase and two of the opposite phase. This is the common case. But if one chromosome pair undergoes disjunction in the first nuclear division and the other chromosome pair waits until the second division before undergoing disjunction the result will be four nuclei with four different combinations of the sexual factors, i.e. four sexual phases in the same promycelium. This doubtless occurs in the other smut species also. The sexuality of smuts has been studied also by Paravicini, Bauch, Dickinson, Kniep, Sleumer and others.

Hüttig has shown that in *Ustilago avenae* the temperature has considerable effect upon the proportions of disjunction in the first and second meiotic divisions. Disjunction in the first division (called by him prereduction) occurred in 14 percent of the cases at 9°, 17.4 percent at 19; 31.5 percent at 25.5°, and in 18.7 percent at 29.5°. Various chemicals also modified these proportions.

Union of opposite sexual strains may take place by the conjugation of two sporidia, the nucleus of one passing into the other sporidium. When this germinates it gives rise to a dicaryon mycelium. Both Dickinson and Boss have shown that the dicaryon phase initiated by the union of two sporidia is often only transitory in culture the further growth of the mycelium consisting of monocaryon hyphae, some of one, some of the other sexual phase. For such species it seems probable that only when the union occurs in the tissues of the

host is the dicaryon phase permanent. This binucleate sporidium may produce a binucleate conidium. Rawitscher and others have shown that instead of producing sporidia the promycelial cells of opposite sexual phase may conjugate by short conjugation tubes, through which the nucleus of one of the cells will pass into the other promycelial cell (Figure 92, *H*, *I*). This latter then produces binucleate sporidia. Or it may happen that uninucleate sporidia will germinate and produce monocaryon mycelium. When two hyphae of such monocaryon mycelia of opposite sexual phases meet they will unite and a dicaryon mycelium will result. A uninucleate conidium from one mycelium may unite with a hypha of a mycelium of opposite sexual phase, etc. Bauch has shown that in *Ustilago violacea* the two sexual phases of mycelium differ in their reaction to various nutrients present as evidenced by the degrees of growth and distribution of the mycelia of the two phases in various culture media, both differing from the mode of growth of the dicaryon mycelium produced when the two cultures are allowed to grow together. Dickinson has shown for *Ustilago levis* causing smut on oats that infection does not take place unless mycelia of two opposite sexual phases are present. Single sporidial cultures will not infect the host plants. It must be noted that Flerov studied a strain of *U. avenae*, also causing a smut on oats, in which a monocaryon sporidium brought about infection by a monocaryon mycelium which eventually produced uninucleate teliospores in which no nuclear fusion occurred. From such teliospores arose a two-celled promycelium. Boss found the same to be true for *Ustilago ischaemi*. These are similar to the monocaryon strain of *Kunkelia nitens* in the Uredinales studied by Dodge. Hanna has demonstrated for *U. zeae* on maize that single sporidia or conidia from cultures from single sporidia are able to infect the tender meristem with a very slender germ tube composed of monocaryon cells. This infection is of very limited extent and no smut galls or teliospores are produced. When two sporidia of opposite sexual phase infect the tissue in rather close proximity the slender monocaryon hyphae approach one another and unite and thenceforth develop as a very stout mycelium of dicaryon cells which penetrates the meristem in all directions. These hyphae show numerous clamp connections. Eventually a smut gall is produced, filled with numerous teliospores. Similar conditions exist according to this author in *Sorosporium reilianum*,

another species producing smut galls on maize. Christensen found three strains of maize smut in which infection and production of large galls occurred with monosporidial cultures. He did not follow the cytological phenomena of these strains within the host. Aside from the distribution of the two sexual phases in the promycelial cells of *Ustilago levis*, Dickinson studied the distribution of the factors for color of the mycelium and for form of the colony when grown in culture. These studies were made by isolating and culturing the sporidia, noting their position on the promycelium. The smut used was a cross of strains possessing yellow and white mycelium and colonies corrugated or depressed. Out of 22 such isolations the sexual strains *A* and *B* occurred in the following order from the apex toward the base of the promycelium: *AABB* (3 times), *BBAA* (five times), *ABAB* (6 times), *BABA* (twice), *ABBA* (3 times), *BAAB* (3 times). The distribution of the other two allelomorphous factors was apparently entirely independent of the distribution of the sexual strains and of each other.

Dickinson, Hanna and Popp and Kniep have made hybrids between different species of Ustilaginaceae. Bauch has demonstrated the occurrence of geographic races in *Ustilago longissima*. In these there is evidence that multiple allelomorphism occurs in both the *A* and *B* factors.

The family includes over 450 species, in about 12 genera. The largest genus is *Ustilago* with over 300 species. Its spores are produced singly in a powdery mass. Many serious enemies of cultivated plants are found in this genus, e.g. *U. avenae* and *U. levis*, destroying the spikelets and inflorescence of oats (*Avena sativa*), *U. zeae* producing smut galls on maize (*Zea mays*), *U. hordei* (Figure 92) and *U. nuda* on barley (*Hordeum sativum*), *U. tritici* on wheat (*Triticum* spp.), *U. striiformis* on *Poa pratensis*, *U. violacea* on *Dianthaceae*, etc. *Sphacelotheca* differs from *Ustilago* in having the powdery mass of teliospores surrounded by a pseudoparenchymatous layer of fungus tissue. *S. sorghi* is injurious to the ovaries of various species of sorghum (*Holcus sorghum* or *Andropogon sorghum*). In *Schizonella* the teliospores are in twos, otherwise much as in *Ustilago*. *S. melanogramma* produces long black sori in the leaves of various species of *Carex*. In *Sorosporium*, *Tolyposporium* (Figure 93, *A*, *B*) and other genera the teliospores are united into more or less firm balls. They are largely parasitic on grasses.

FAMILY TILLETIACEAE.—Promycelium non-septate, the sporidia being clustered at its apex in a dense cluster or in a whorl (Figure 93, C, F). The number of sporidia varies from 4 to 30-50. The teliospores arise as terminal cells of hyphae or of short lateral branches or

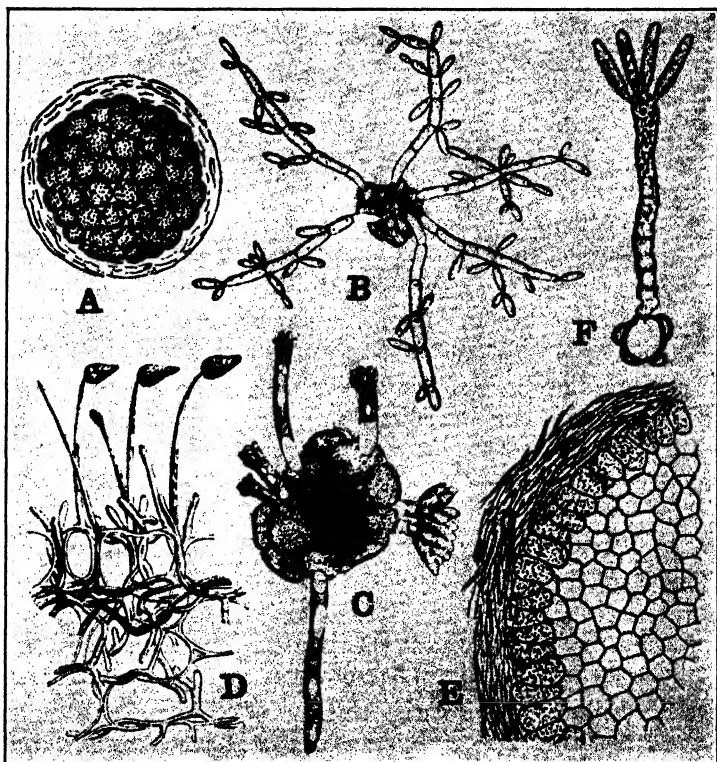


FIG. 93.—Ustilaginales. A, *Sorosporium saponariae*; B, *Tolyposporium junci*; C-D, *Tubercinia trientalis*, C, germinating spore ball; D, conidial development on host leaf; E, *Doassansiopsis marianoffiana*; F, germinating spore ball of *Urocystis occulta*. (A and E after Dietel in Engler and Prantl, 1898; B after Brefeld, 1895; C and D after Woronin, 1882; F after Stakman, Cassell and Moore, 1934.)

as intercalary cells. The two nuclei unite and the cells round up and secrete a heavier wall, which may be dark or light in color and is smooth or more often reticulately marked or spiny. The teliospores occur as single cells in a dusty mass, or united into small or large balls of spores with or without a covering or a core of sterile cells. These spores or spore balls may escape as a powdery mass or may

remain within the host tissue. The sporidia are fusiform or sickle-shaped and are inclined to unite by twos while still attached to the promycelium or after they have fallen off. As in the preceding family the sporidia appear to be of at least two sexual phases. From one of the sporidia of the united pair a germ tube of dicaryon cells is given off and infects the host plant, or infection takes place from a dicaryon conidium set free from a dicaryon mycelium. The sexual cycle which is initiated by the fusion of the sporidia is completed by the union of the nuclei in the teliospore.

About 13 genera and over 250 species are recognized in the family. *Tilletia* (about 40 species) corresponds to *Ustilago* in producing its teliospores as single cells forming a powdery mass. *T. tritici* (with rough teliospores) and *T. levis* (with nearly smooth teliospores) cause stinking smut or bunt of wheat. Flor has crossed these two species by picking off single sporidia and allowing the two monocaryon mycelia produced from them to unite. These hybrid mycelia were used successfully to inoculate wheat plants. The teliospores produced on these plants resembled most closely those of *T. levis*. Certain species of *Tilletia* have been described from the capsules of *Sphagnum* and *Anthoceros* among the Phylum Bryophyta, but since the germination of the spores has not been observed it is not at all certain that this genus or even this family is concerned. *Entyloma* produces its teliospores singly in the tissues of the host from which they do not escape as a powdery mass, but germinate within the host sending their elongated promycelia through the epidermis and forming the sporidia externally. Conidia are also formed on conidiophores which emerge through the stomata. The 100 or more species are found on Grasses (Poaceae), Ranunculaceae and other families, but particularly on the Compositae (Asteraceae). *Urocystis* (about 60 species) produces its teliospores in balls of from 2 (rarely 1) to 4 or 5, the ball being partly or completely surrounded by a layer of small sterile cells. The mass of spore balls is powdery and the latter escape upon rupture of the host tissue. *U. occulta* (Figure 93, F) causes longitudinal lead-colored, slightly raised sori on the stems and leaf sheaths of rye (*Secale cereale*), the head being killed by the presence of the fungus in the stalk below, it being rarely entered by the fungus. *U. violae* and *U. anemones* form their sori in the leaves respectively of *Viola* and of various species of the

Ranunculaceae. In *Tubercinia* (Figure 93, C, D) all the cells of the spore ball are fertile spores. About 20 species of *Doassansia* are known producing galls on the leaves of various Alismataceae and related aquatic plants. The large spore balls have very numerous teliospores and an external layer of hyaline sterile cells. *Doassansiosis* (Figure 93, E), also on Alismataceae, produces large spore balls made up of a central core of hyaline pseudoparenchymatous cells surrounded by a single layer of larger dark teliospores, these in their turn being surrounded by a filamentous sheath.

The true affinities of the Teliosporae are a matter of dispute. In the Order Auriculariales of the Class Basidiomyceteae (in the narrower sense as used by the author) basidia are produced which become transversely septate into four cells, each of which produces a basidiospore on the end of a sterigma (Figure 94, B; 99; 100, F, G). The spore-fruit is usually gelatinous. With but few exceptions the species are saprophytic upon wood. These exceptions are parasitic upon insects and mosses and possibly ferns and grasses. Because of the similarity of the basidium of this order to the promycelium of the Teliosporeae Brefeld and others following him placed the Ustilaginales as the lowest group of Basidiomyceteae, next to the Phycomyceteae from which they were held to have arisen. Next above these they placed the Uredinales and from them the Auriculariales were believed to have been derived, these in turn having given rise to the remainder of the Basidiomyceteae. Undoubtedly there is a relationship between these three orders but there are what the author considers valid objections to the foregoing arrangement. It is difficult to conceive that such highly specialized parasites as the Smuts and Rusts could give rise to the mainly saprophytic groups of Basidiomyceteae. Other mycologists have avoided this difficulty by suggesting that the Rusts and Smuts are offshoots from the Auriculariales by simplification and reduction of the spore fruit and a specialization of the life history under the influence of intense parasitism. This accords with the serological studies of Neuhoﬀ and Ziegenspeck, students and colleagues of Carl Mez. So Fitzpatrick points out that *Eocronartium muscicola* parasitic upon mosses, and other moss and fern parasitizing Auriculariales may well stand near the ancestral line of the rusts. The complete absence of spermatogonia as well as of receptive hyphae (trichogynes) in the Auriculariales so far

as present studies go makes it difficult to see just how the Rusts could have arisen directly from these fungi although this objection would not hold for the Smuts.

In the Basidiomyceteae (*sensu strictiore*) the basidia are the terminal, at first binucleate, cells of dicaryon hyphae, arranged in a hymenial layer. The teliospores are also terminal (in most cases) binucleate cells of dicaryon hyphae and in the Rusts at least may be approximated in a sort of hymenial layer (e.g. *Melampsora*). It is from these cells that the promycelia arise. The promycelium plus the teliospores correspond to the typical basidium. In two genera of the Auriculariales a structure somewhat similar to this is found (Figure 99), but there is no indication of the other structures characteristic of the Uredinales. Admitting the general relationship, the author is compelled to believe that the ancestors of the Teliosporeae arose from the Ascomyceteae at an early date and that very early there arose a divergence of the Teliosporeae on the one hand as parasites retaining (at least in the Rusts) such Ascomycetous structures as the spermatogonia, receptive hyphae, etc., and of the Basidiomyceteae on the other hand, largely as saprophytes. The dicaryon mycelium of the Rusts and Smuts corresponds to a well developed series of ascogenous hyphae. Therefore the suppositious ancestral Ascomyceteae must have been forms with spermatogonia, trichogynes, free sperm cells, and well developed ascogenous hyphae. The Taphrinales have a dicaryon vegetative mycelium arising in much the same way as that of *Ustilago zeae* and *Tilletia*, but the monocaryon phase is almost lacking and there are no spermatogonia. We must look somewhat lower, probably to some of the more primitive Pezizales for the suppositious ancestor. We must then assume that the endoascus spores (ascospores) have been replaced by external spores. It is conceivable (but the connecting steps are not known) that tightly packed or intramatrical asci germinated as a whole into a tube which upon emerging into the air became septate and externally spore bearing. Thus would arise the promycelium type of structure, as well as the basidium such as found in some of the Auriculariales.

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CHAPTER XI

BASIDIOMYCETAE

INTRODUCTION AND HETEROBASIDIAL ORDERS

The Basidiomycetae, in the sense used by the author, are characterized typically by the production of basidia in a hymenium. This hymenium may be exposed to the exterior, either directly or indirectly, or may form the lining of closed cavities. In some groups the hymenium is obliterated by the irregular arrangement of the basidia. These hymenia are borne upon or within spore-fruits of usually considerable complexity and often of great size. The form, consistency and structure of these spore-fruits are varied to the highest degree and are, together with the structure of the basidium, the bases for the classification of the group. Usually two phases of mycelial development can be distinguished: primary (monocaryon) and secondary (dicaryon) mycelium. The latter very frequently has clamp connections (to be described later) but these are entirely lacking in some whole families and absent in occasional smaller groups throughout the class. Conidia are produced in some forms but it has not been determined whether they are present on both forms of mycelium or confined to the primary or secondary mycelium only. They are mostly colorless and ellipsoidal or spherical and smooth, or less often warty or spiny and colored, and arise from simple, short, or more or less elongated and branched conidiophores. To a very great degree the Basidiomycetae are saprophytes, upon organic matter in the soil, decaying leaves, dung or wood. Parasitism upon green parts of plants is known in several orders, but such cases form a very small minority. A few are parasites upon insects or upon fungi. Of the wood-inhabiting species some are the cause of great damage to structural timbers, lumber and even to living trees. Even though the fungus may be confined entirely to dead wood (e.g. the heart wood or the no longer living wood fibre cells of the sap wood) the rotting of the wood may so weaken the trunk that the tree falls. In living trees access to the

wood by the spores of the fungus is usually obtained through wounds caused by the breaking or death of limbs, boring of insects or injury to the bark by falling trees, etc. In some cases the fungus mycelium passes from tree to tree through the soil, entering the roots which it may kill, thus bringing about the death of the tree.

The basidia are of various shapes and structure. The extensive studies of Dangeard, Ruhland, Harper and others demonstrate that they arise at the ends of hyphae of dicaryon cells (very rarely several cells below the terminal cell may also successively become basidia). The cell enlarges as do the two nuclei which then unite to form a relatively large diploid fusion nucleus which undergoes two (meiotic) divisions to form four haploid nuclei. Subsequent divisions may increase the number of nuclei to eight or more, but four and eight are the most frequent numbers. From the side or more often from the apex of the basidium spores bud out on short or long sterigmata and through the latter a nucleus passes into each spore. Mostly the four nuclei pass into four basidiospores leaving the basidium empty but frequently the four nuclei divide just before spore formation, one daughter nucleus passing into each of the four spores and four remaining in the basidium. Bauch has shown that not rarely only two of the normally four nuclei pass out into spores or that two nuclei pass into each spore so that two-spored basidia are produced. These are not to be confused with the two-spored basidia which arise parthenogenetically from monocaryon mycelium in a few cases. In such basidia the single primary (haploid) nucleus divides by mitosis (not meiosis) into two nuclei which pass out into the basidiospores. This case corresponds to the monocaryon strain of *Ustilago avenae* grown by Flerov and to *Kunkelia nitens* studied by Dodge, and mentioned in the preceding chapter. In some members of the class six or eight or even twelve basidiospores are produced on each basidium, and in a few cases only one basidiospore is produced.

In many Basidiomyceteae the spindle of the first nuclear division in the basidium is longitudinal or obliquely longitudinal. Each daughter nucleus then divides in its place with its spindle also more or less longitudinal. Basidia of this type were called by Juel stichobasidial. The nuclei are arranged in a more or less longitudinal row but may then move to the upper end of the basidium and pass into the basidiospores with or without dividing again. In the

chiastobasidial type of basidium the first nuclear division occurs near the apex of the basidium (rarely nearer the middle) and the spindle is transverse as are the spindles of the next division, but at right angles to the axis of the first spindle. Because of the fact that to a large extent these two types are correlated with other differences Juel, Maire, Gäumann and others have considered this to be a difference of profound importance. However, since transitional forms have been found by Levine in the genus *Boletus* and both types of nuclear division have been observed by Eftimiu and Kharbush in different basidia in the same hymenium of *Exobasidium rhododendri* it is apparent that this can not be used as a primary character in a system of classification.

In structure the basidia may be divided into four types, recognizing that there are more or less transitional forms between these types. The form typical for over 95 per cent of the species of the class consists of unicellular basidia with spores sessile or on sterigmata which are very slender in proportion to the size of the basidium and of the spore. In the majority of species these basidia are clavate, much like the asci of *Peziza*, with the four basidiospores attached to short sterigmata at points near the apex (Figure 104). This is true especially of the forms with external hymenium (Order Agaricales). In the forms with enclosed hymenial cavities (the Gasteromyceteae) the basidia, though often of this type are frequently round (Figure 129, A). In the genus *Tylostoma* the four basidiospores are produced from the sides of the basidium at various distances from the apex (Figure 129, B). The groups producing this type of basidium are sometimes called the Eubasidiae or Homobasidiae. The basidiospores of these groups usually germinate directly by a germ tube.

In the second type, as is true for all types of basidia, the young basidium is two nucleate. The nuclei unite and then occur the two meiotic divisions with the spindles longitudinally placed, resulting in the formation of four nuclei scattered up and down the basidium. At the apex of the basidium two stout branches are formed, about equal in diameter and in length to the body of the basidium (Figure 102, B, E). Into them the two uppermost nuclei pass. Through slender sterigmata formed at the tips of the branches these nuclei then pass into the two basidiospores while the other two nuclei remain in the basal portion of the basidium and eventually

degenerate. In some species these basidia resemble a tuning-fork and so this type is sometimes spoken of as the tuning fork type. It is confined to the Order Dacryomycetales.

The third type, characteristic of the Order Tremellales, consists of round basidia with four, usually long and slender or stout branches. The body of the basidium divides by a vertical wall into two cells after the first nuclear division and another vertical wall at right-angles to the first divides these two cells again after the second nuclear division. The nuclear spindles in both divisions are transverse to the longitudinal axis of the cell, i.e. the basidium is of the chiasmatobasidial type. Each branch arises from one of these uninuclear segments and bears at its apex a slender sterigma on which a single basidiospore is borne (Figure 101, C-E).

The fourth type, found in the Order Auriculariales, is one that very closely resembles the promycelium of the Class Teliosporeae, especially that of the Rusts. In the young basidium after the first nuclear division, a cross septum is formed and after the next division other cross walls develop so that a row of uninucleate cells is produced from each of which a sterigma develops, bearing a basidiospore (Figure 94, B, C; 99; 100, B-G). The nuclear spindles are placed longitudinally, i.e. the basidium is stichobasidial. The sterigmata may be short so that the four basidiospores lie in a row down one side of the basidium, as in *Phleogena* (*Pilacre*), or may be elongated and curved upwards so that the basidiospores lie at the same level, as in *Auricularia*. In *Septobasidium* and some related genera the basidium is at first round and with a thin or somewhat thickened wall. From this "probasidium" grows the slender cylindrical portion which becomes septate and upon which the basidiospores are formed (Figure 99). The probasidium is clearly very similar to the teliospore and seems to indicate a close relationship to the Teliosporeae and perhaps parallel development from common ancestors. This affinity was pointed out by Vuillemin in 1893. The probasidium is frequently called the "hypobasidium" and the slender portions growing out from it the "epibasidium." Using this terminology the teliospore and promycelium would be respectively hypobasidium and epibasidium.

The three groups of Basidiomycetes, viz. the Dacryomycetales, Tremellales and Auriculariales, which have these last three types of basidia were called by Patouillard the Heterobasidia. In them the

basidiospores often germinate by lateral sprout cells from which later the typical mycelium develops (Figure 94, *D*; 101, *G*; 102, *C*).

The basidiospores throughout the Basidiomyceteae are universally unicellular when first formed and usually uninucleate (except the rare cases where two nuclei enter the basidiospores from the basidium). In many species the nucleus divides before the spore is set free. In *Dacryomyces* (Figure 102, *C*, *F*) and some other genera the basidiospore becomes transversely septate into several cells

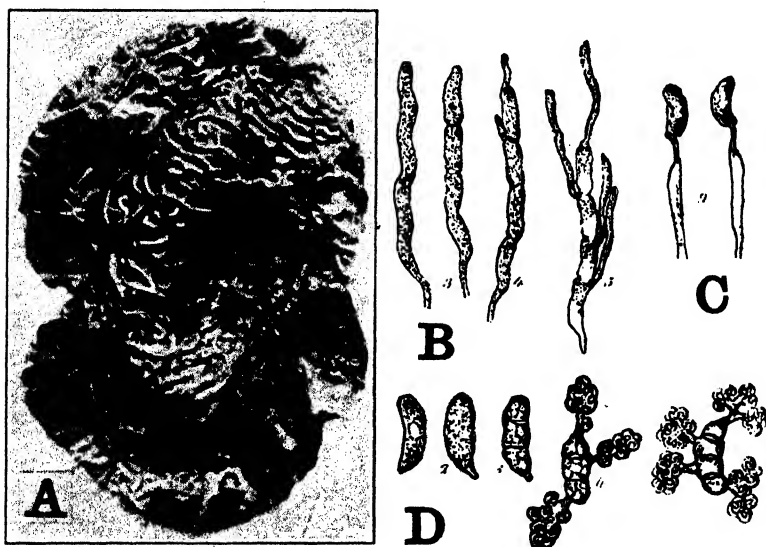


FIG. 94.—Auriculariales. *A*, *Auricularia auricula-judae*; *B*–*D*, *A. sambucina*. *B*, development of the basidium; *C*, epibasidium, sterigma and basidiospore; *D*, germination of basidiospore. (*A* after Möller, 1895; *B*–*D* after Brefeld, 1888.)

shortly after separation from the sterigma. In color the spores in this class vary from hyaline (the majority of species) to pink or to yellow brown, brown, purple-brown and black.

In the Basidiomyceteae with hymenium external at maturity the basidiospores are discharged from the basidia with considerable violence, usually all four spores being discharged successively at intervals of several seconds to several minutes (Figure 95). The distance to which the spores are discharged may be 10 to 20 times the length of the spore. By affixing a clean glass coverslip a short distance from the surface of the mature hymenium (e.g. a gill of a

mushroom) the basidiospores will sometimes be found sticking to the glass in groups of four. In this manner it is possible to obtain and make cultures from the four spores arising from a single basidium. Buller has made very extensive studies of this discharge of basidiospores and its relation to the distribution of the spores by air currents.

In all cases where the basidiospores are expelled violently Buller has pointed out that they seem to be attached somewhat obliquely to the sterigmata. Just before the spore discharge a drop of liquid begins to appear at one side of the point of attachment attaining full size in five to twenty seconds. It is noteworthy that the sporidia

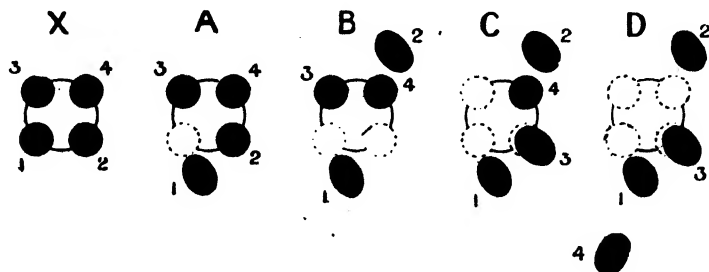


FIG. 95.—Agaricales. The successive discharge of the four spores from the same basidium of *Agaricus campestris*. X, the basidium before the first spore was discharged and A, B, C, and D after each spore had been discharged. The final position of each spore is shown after it was shot off and had fallen back on the hymenium. (After Buller, 1909.)

are attached in a similar manner and that a similar drop is produced in the Uredinales and in the Tilletiaceae, in both of which groups these spores are shot off with violence. This mode of attachment and release is entirely different from that of true conidia.

Aside from the conidia many Basidiomyceteae produce small hyaline, one-celled and uninucleate spores called oidia. They arise on oidiophores and as they are set free they cling together in a drop of sticky liquid, forming little shining balls (Figure 96, A, B). The oidiophores may be simple or branched. The branches or the apical portions of the unbranched oidiophore break up into oidia successively from the tip towards the base, leaving eventually only a short stub. Brodie, Vandendries and others have shown that mostly the oidia arise only from primary (i.e. monocaryon) mycelium. Long ago Dangeard described the formation of uninucleate oidium-like cells from the dicaryon mycelium of *Dacryo-*

myces and recently Vandendries and Martens have demonstrated their occurrence on the dicaryon mycelium of *Pholiota aurivella*. In this species from the same secondary mycelium may be produced thick-walled binucleate "gemmae" and thin-walled binucleate "oidia," both of which give rise to dicaryon mycelium, and also uninucleate oidia. The latter begin as binucleate, spindle-shaped cells which become divided by a cross septum into two uninucleate

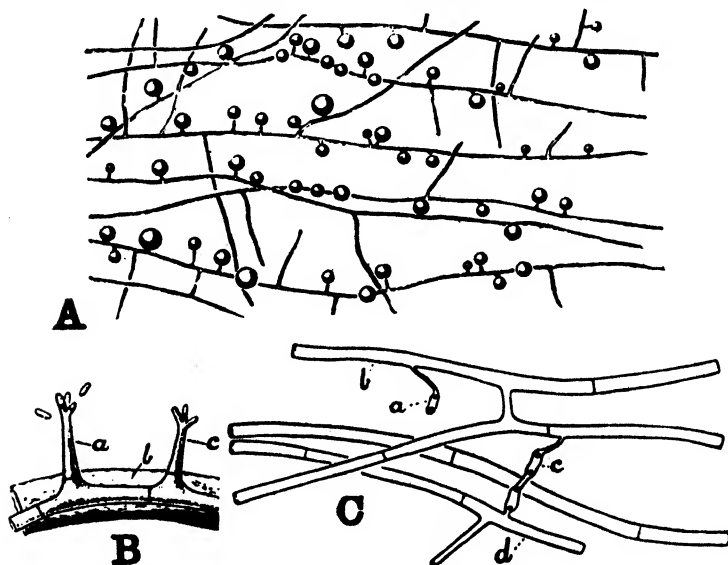


FIG. 96.—Agaricales. Sexual reproduction in *Coprinus lagopus*. A, monocaryon mycelium bearing heads of oidia; B, detail of oidiophore; C, oidia (a and c) of one sexual phase fusing with mycelium (b and d) of opposite (compatible) sexual phase. (After Brodie, 1931.)

cells which fall apart to form the uninucleate oidia. These latter, upon germination, give rise to monocaryon mycelium. The sticky droplets containing the oidia attract insects in the same manner as do the sticky drops from the spermatogonia of the Rusts. Brodie has demonstrated that small flies carry these oidia from monocaryon mycelium to monocaryon mycelium. In *Coprinus* and many other Basidiomyceteae the fungus occurs in two sexual phases. It has been shown by Vandendries and by Brodie that the oidia from one phase are able to fertilize the mycelium of the opposite phase, as is the case in the Rusts. The germinating oidium unites with a cell (Figure 96, C) of the monocaryon mycelium and thus initiates the

dicaryon stage of growth. Either this dicaryon cell grows out into a dicaryon hypha or the nucleus introduced by the oidium divides and a daughter nucleus passes through the wall into the next cell and so on until the whole hypha is "diploidized" as demonstrated by Lehfeldt and by Buller. When the introduced nucleus or one of its descendants arrives in the terminal cell of a hyphal branch the two nuclei divide by conjugate division and thenceforth a typical dicaryon mycelium is produced from this hypha. The initiation of the dicaryon phase does not depend alone upon the oidia. Two

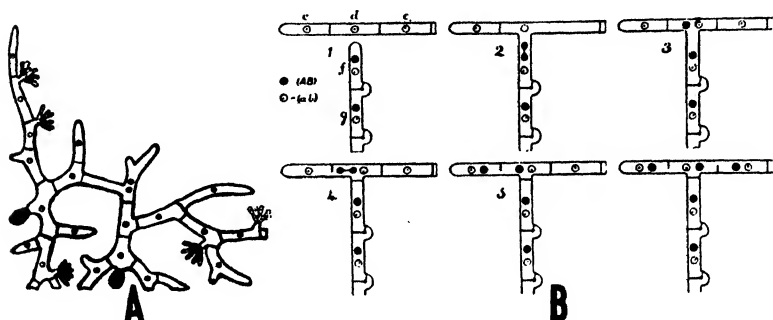


FIG. 97.—Agaricales. Diploidization of monocaryon mycelium. A, two monocaryon mycelia, mutually compatible, have united and diploidization has been initiated in one cell; B, 1-6, diagrammatic representation of the steps in the diploidization of a monocaryon mycelium by a dicaryon one. (After Buller, 1930.)

monocaryon hyphae of opposite sexual phase may unite and the result is the same as when an oidium unites with a hyphal cell (Figure 97, A). Brodie demonstrated that the oidia of *Coprinus lagopus* are capable of germinating and forming a mycelium made up of very slender monocaryon hyphae. From these arise very numerous oidiophores and heads of oidia. When two such oidial mycelia of opposite sexual phase meet diploidization occurs. Also the oidia from one mycelium may fertilize the oidial mycelium of the opposite sexual phase. The oidia and the oidial mycelium may represent a residual male sexual structure while any cell of the normal monocaryon vegetative mycelium possesses a female tendency, this not being restricted merely to an oogone as in many of the Ascomycetae. Vandendries and Brodie find, however, that in some Basidiomycetae the oidia are also capable of functioning as conidia, producing a typical monocaryon mycelium which is

capable of diploidizing and being diploidized by a monocaryon mycelium of appropriate sexual phase.

Miss Bensaude and Kniep were among the first to show the existence of different sexual phases (or as they called it "heterothallism") in the Basidiomycetae. Miss Mounce and Miss Newton and various other investigators have shown that many of this class are "homothallic" i.e. will produce the dicaryon mycelium in culture from a single basidiospore while other species are always "heterothallic." Rarely a monocaryon mycelium of a "heterothallic" species after a considerable time begins to produce dicaryon hyphae in a manner not yet satisfactorily explained. In the "homothallic" species where the basidiospore is uninucleate it must be assumed that the genetic factors for incompatibility are absent or are both present and mutually canceling in the same chromosome. Sass has studied the behavior of the nuclei in certain homothallic forms in which the nuclei are two in number in the basidiospore. Thus in *Coprinus ephemerus* there exist forms in which four uninucleate basidiospores are produced on each basidium; these forms are "heterothallic." In *C. ephemerus* forma *bisporus* only two basidiospores are produced each with two nuclei. Mostly these give rise to homothallic mycelium but sometimes show heterothallism. Sass found that from 90 percent of such binucleate spores there is produced a coenocytic mycelium which as it grows begins to become septate until the apical portions of the hyphae consist of uninucleate cells. Some of these hyphal branches on coming into contact with other uninucleate hyphae from the same mycelium fuse with them to form typical dicaryon mycelium (with clamp cells) and from this mycelium arise the normal fruiting bodies. Evidently the two nuclei of the basidiospore represented opposite sexual phases. In about ten percent of the basidia the two nuclei of the spore are evidently of the same sexual phase. Such spores produce a mycelium consisting from the first of uninucleate cells. Only when two such mycelia of opposite sexual phases come into contact is the secondary, fruiting mycelium produced. The situations described by Sass are very similar to those reported by Ames in *Pleuraea anserina* (See Chapter VIII).

As in the case of *Ustilago zeae* described in the preceding chapter the four basidiospores may represent two or sometimes four sexual phases which are mutually fertile by twos. Because of the presence

of male sexual organs (oidia) on the mycelium of both uniting mycelia and of the fact that each mycelium or its oidia can diploidize the other mycelium it is manifest that we can not look upon these as representing opposite sexes. As in the Rusts it is a question of self incompatibility, comparable in a way to that occurring within a given horticultural variety of pear which may be sterile to its own pollen but fertile to pollen of another (but not of every other) variety. Since the term heterothallism as originally applied refers to mycelia representing actual different sexes it seems inadvisable to use the terms heterothallic and homothallic in these higher fungi, at least without qualification.

Apparently the factors governing the compatibility are two allelomorphic factors borne on different chromosome pairs. Kniep and others have pointed out that only those unions of cells lead to diploidization that bring about a combination that is heterozygous for both these sets of factors. This need not involve a union of the nuclei into a diploid nucleus, a process that occurs only in the basidium, but concerns merely the bringing together, without union, of two haploid nuclei in the same cell, so that so far as the cell is concerned diploidization has taken place even though the two haploid nuclei remain separate for the present. Thus a monocaryon mycelium with the compatibility factors A and B (these being on separate chromosomes) could unite with another monocaryon mycelium of the formula ab ; similarly a mycelium with the formula aB could unite with one of the formula Ab . In either case the formula for the resultant cells would be $AaBb$, a condition heterozygous for both sets of characters, and fulfilling the requirements for the mating of the mycelia. In the basidium the diploid nucleus undergoes two meiotic divisions to consummate the reduction process. If both pairs of chromosomes bearing the factors for incompatibility or compatibility undergo disjunction in the first division it will be a matter of chance whether the resulting daughter nuclei will be Ab and aB or AB and ab . Since each nucleus divides again, this time by splitting of the chromosomes, there will be four nuclei (one for each spore), two each of the formula Ab and aB or AB and ab respectively. If the disjunction does not occur in either chromosome pair until the second meiotic division the first division will represent merely a splitting of the chromosomes so that the two daughter nuclei will be like the parent nucleus with the formula

AaBb. When these divide by the disjunction division this time it will give *Ab* and *aB* or *AB* and *ab*, for each of the two nuclei. If the separation of the chromosomes of the chromosome pairs occurs in the same direction in both nuclei there will result four nuclei, alike two by two, but this separation may be in opposite directions in the two dividing nuclei for one of the chromosome pairs so that the four nuclei may all be different. If disjunction of one chromosome pair occurs at the first division and of the other pair at the second division the four resultant nuclei will be all different, viz. *Ab*, *aB*, *AB*, *ab*. Miss Newton has shown that in *Coprinus lagopus* all of the foregoing arrangements may be found in the various basidia of the same hymenium. Apparently disjunction occurs more often at the first division for both sets of chromosomes, for in the majority of cases two of the basidiospores of a given basidium will be of one sexual phase and the other two of the opposite phase. In some species only two sexual phases appear to occur. These are spoken of as possessing bipolar sexuality in contrast to those species with quadripolar sexuality such as described above. In a bipolar species only one allelomorphic pair of incompatibility factors need be assumed.

Not infrequently a monocaryon mycelium may produce spore-fruits, but in this case the basidia are less numerous and are either sterile or give rise to but two, uninucleate basidiospores, both of the same sexual phase as the parent mycelium. In *Coprinus fimetarius* Oort has shown that two monocaryon mycelia may intermingle and together build spore fruits when they represent phases alike genetically for one factor and heterozygous for the other, e.g. $Ab \times AB$. Such fruits are not normal but may produce two kinds of two-spored basidia which are about equally divided between the component phases, in this case *Ab* and *AB*. It is apparent that no true sexual union has occurred in such a case. That this is more than a simple intermingling of separate monocaryon mycelia is demonstrated by the fact that clamp connections may be formed, varying from incomplete or abnormal structures to those of perfectly normal appearances. The latter vary from only occasional to frequent. The external conditions appear to have considerable effect upon the number of clamp connections produced. This is comparable to what Bauch showed to occur in the Ustilaginaceae. These unions do not arise in all the incompatible combinations. Van-

dendries and Brodie show that in *Hypholoma candolleianum*, a quadripolar species, the mycelia to which they ascribe the formula ab' when mated with $a'b'$, or ab when mated with $a'b$ cause mutual partial inhibition of growth so that when growing close together they are much smaller than when grown apart or in the combination $a'b \times a'b'$. The latter corresponds to the combination studied by Oort which produced the combination spore-fruit. Oort also found that such spore-fruits were not produced in certain combinations. Vandendries and Brodie have described also what they term "barrage sexuel." This had been noted before by Oort and by Brunswik but not studied intensively. This amounts to a mutual repulsion of the hyphae of some of the incompatible matings. When two such cultures are established in the surface of an agar medium the mycelia as they grow leave a gap between the two cultures. This is especially marked in the aerial mycelium whose hyphae show abrupt curvatures when they approach the other mycelium at a distance of 3 to 5 mm. These authors showed further that the interposition of thin plates of glass did not prevent this repulsion nor did sheets of mica, very thin sheets of silver, lead and other substances. Apparently the repulsion is due to some sort of ray emanating from the mycelium. Experiments show that certain nuclear combinations give these mycelial repulsions but not others. Thus the combinations $ab \times ab'$ and $a'b \times a'b'$ show "barrage" but not $ab \times a'b$ or $ab' \times a'b'$. Clearly the repulsion is between the b and b' mycelia. The repulsion was also demonstrated between dicaryon mycelium and monocaryon mycelium and between dicaryon mycelia where the two sets of nuclei were different, e.g. $(ab + a'b') \times (a'b + ab')$. This "barrage" as well as the inhibition of growth does not occur in all species.

A peculiar phenomenon in connection with the occurrence of bipolar and quadripolar sexual phases is that of "geographic races." This has been studied by Hanna and by Vandendries and extensively by Brunswik. In some species of *Coprinus* the two sets of incompatibility factors may be alike in fungi growing in the same locality but one or both sets may be different in fungi (of the same species) growing in different localities. In the latter case all sexual phases of one fungus would be compatible with all sexual phases of the other fungus, while in the former case (only one pair different in the two fungi) certain combinations will be incompatible. This is very

similar to what Bauch found in *Ustilago longissima* in which various geographic allelomorphs of both *A* and *B* factors were studied. Such occurrences are sometimes reported as "multipolar" sexuality.

In the majority of the Basidiomyceteae and apparently in some of the Ustilaginaceae the dicaryon mycelium can be distinguished from the monocaryon mycelium by the possession of clamp connections. Their origin was ascertained at about the same time by Mlle. Bensaude and by Kniep, studying independently.

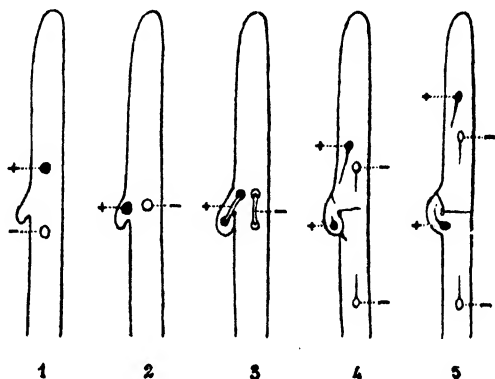


FIG. 98.—Agaricales. 1-5, diagrammatic representation of the steps in the formation of a clamp connection. The nuclei of the opposite sexual phases are shaded differently. (After Mlle. Bensaude, 1919.)

The details of the formation of a clamp connection are as follows (Figure 98): The two nuclei of the terminal cell of a dicaryon hypha lie a short distance apart in the narrow lumen of the cell. Between them a lateral pocket is formed in the wall. The two nuclei now divide simultaneously (conjugate division) and the lower daughter nucleus of the upper pair passes into the pocket. This is now cut off from the main cell by the formation of a septum. At the same time the upper daughter nucleus of the lower pair, lying at about the level of the upper end of the pocket is separated from its sister nucleus by a transverse wall. At this stage the terminal cell has again two nuclei, the cell below has one nucleus, while a fourth nucleus lies in the lateral pocket. The latter curves around until it is in contact with the lateral wall of the upper end of the penultimate cell and the intervening walls are dissolved and the nucleus passes into the latter cell. The lateral pocket has acted as a by-pass through which a nucleus has been transferred from the terminal to the penultimate

cell in such a manner as to provide each cell with a daughter nucleus of each of the two nuclei originally in the terminal cell. This by-pass is known as a "clamp connection." Buller has followed the formation of these clamp connections in living mycelium and finds that the process requires only a short time. In *Coprinus lagopus* the time elapsed from the first appearance of the projecting lateral pocket until the passage of the nucleus out of the pocket into the penultimate cell was 23 minutes, while in *C. sterquilinus* it was 40 to 45 minutes. The conjugate division of the nuclei was completed in the first species in from 12 to 14 minutes.

The phenomena involved in the formation of the clamp connections are generally considered (e.g. by Kniep, Bensaude, etc.) as being homologous to those occurring in an ascogenous hypha when an ascus is forming by the hook method. The Moreaus have shown that the formation of the hook does not necessarily lead immediately to the formation of an ascus, for the terminal binucleate cell may elongate and again form a hook while the tip of the hook unites with the cell below. This may continue several times until a series of dicaryon cells is produced, each connected to the cell below by a clamp connection. The similarity may be even greater when the terminal cell instead of curving over to form a hook merely sends out a lateral pocket. It should be noted that Mattiolo described and figured in 1888 typical clamp connections on what he considered to be the mycelium of *Tuber lapideum* (Figure 60, E). Unless he mistook some intermingled strands of Basidiomycetous mycelium for that of the fungus he was studying the occurrence of this structure in the Ascomyceteae as well as in the Basidiomyceteae must be considered substantiated.

Buller does not believe that the formation of clamp connections is at all homologous to the processes occurring in the ascogenous hyphae. The clamp connections play, he believes, an important part in the transfer of food through the mycelium. An actual flow of protoplasm was observed by him through the clamp connection and its perforated upper septum. Possibly the occurrence of whorls of clamp connections in some fungi would support Buller's view on their function in nutrition.

The greater prevalence of clamp connections in the Basidiomyceteae is probably due in the first place to the fact that in most members of this class the dicaryon mycelium represents a much

greater portion of the life history of the plant than do the rather transitory or entirely wanting ascogenous hyphae of the Ascomyceteae. Furthermore, in the latter group these hyphae are broader in general, so that at conjugate division the two dividing nuclei may lie side by side instead of some distance apart in the longitudinal axis of the narrow hypha. Only in the latter case is a by-pass really necessary. Some whole families of Basidiomyceteae lack clamp connections entirely while in some genera the clamp connections are several, in a whorl, at each septum. Whether this plurality of clamp connections is for better transfer of food, as suggested above, or has to do with the occurrence of several pairs of nuclei in the dividing cell is not known.

The prevalence of clamp connections varies greatly in different parts of the same mycelium and is, furthermore, modified greatly by the environment. Thus mycelium submerged in liquid media may have but few or even no clamp connections while the aerial portions may produce them in abundance. They may be present on the more slender hyphae in the pileus of a mushroom and absent in the broader extensions or branches of these same hyphae. In some species they are found only at great intervals while in others they occur at every septum. In some species they are only found in the subhymenial tissues of the spore-fruit but not elsewhere, even when all the tissues consist of dicaryon mycelium. Hirmer observed conjugate divisions in the mycelium of *Agaricus* (*Psalliota*) *campestris* although clamp connections were completely absent. Within the genus *Coprinus* Brunswik has found some species which lack the clamp connections entirely and other closely related species in whose mycelium they are abundant. He interprets this as a gradual loss of a structure inherited from the Ascomycetous ancestors but whose function is no longer indispensable.

The arrangement of the orders and families of the Basidiomyceteae in any attempted natural system of classification must depend largely upon the views entertained as to the ancestry of the class. The system most frequently followed is that put forth by Brefeld and forms the basis of the system of Killermann in the second edition of Engler and Prantl. This is based upon the idea that the basidium is a modification of a conidiophore such as is found in some of the Phycomyceteae, from which class Brefeld believed the Basidiomyceteae to have descended directly. The conidiophores are

supposed to have been provided at first with an indefinite number of cells and conidia. It is assumed that the number of cells became fixed at four, at first with several conidia to a cell (e.g. several sporidia to each promycelial cell of the Ustilaginales), and finally, with the failure to form septa, the conidiophore became a one celled, four spored structure (the typical basidium). However logical such a classification appears, its fundamental falsity has been made apparent by the cytological studies of Dangeard, Maire, Ruhland, Harper and many others which have shown that the basidium is a (usually) terminal cell of a dicaryon hypha whose nuclei unite and undergo two (or more) divisions. Furthermore the mycelial cell divisions are accompanied by the production of clamp connections, these phenomena being identical with those found in the ascus and ascogenous hyphae. It is then to the Ascomycetae that we must turn to find the ancestors of the Basidiomycetae, it being necessary to assume that the spore formation has become external instead of internal, a suggestion made many years ago by Vuillemin.

Since the usually abundant dicaryon mycelium of the Basidiomycetae appears to be homologous to the ascogenous hyphae of the Ascomycetae we must seek the ancestral forms in a group of the latter class in which ascogenous hyphae are abundantly developed. In the main the hymenium is external and extensive in the Basidiomycetae so that we would expect it to be rather well developed in this ancestral group. Fertilization by sperm cells (oidia) most probably occurred in this group since we find it well established in a few of the Basidiomycetae. These features are all found in the Pezizales or closely related groups. In the Taphrinales (Exoascales) the whole vegetative mycelium is of the dicaryon type but no clamp connections or ascus hooks are present (at least in the Taphrinaceae, the condition existing in the Ascocortiaceae being unknown). This group, therefore, seems not to be in the direct line of ancestry for the Basidiomycetae. Yet it seems probable that those forms of the latter group, with rather effuse superficial hymenium, which have the closest superficial resemblance to the Taphrinales, must represent the more primitive groups. The Class Teliosporeae must be placed as a group closely paralleling the more primitive Basidiomycetae and probably branching off from their early ancestral line. Thus would be justified the contention of those who would include the Teliosporeae within the Basidiomycetae, if the manifest

specialization of the former as internal parasites as well as the other differences already discussed are considered not sufficient to warrant the erection of a separate class.

In the arrangement followed below it is not to be considered that this represents a single progressing line of evolution. On the contrary the first three orders (forming the Heterobasidiae of Patouillard) are groups with a more or less parallel evolution from primitive forms that have been lost (and which lie close to the primitive forms ancestral to the Teliosporeae). In the Eubasidiae (or Homobasidiae of Patouillard) the Agaricales are also rather parallel in their evolution but, with the much more efficient basidium, extend much further, progressing finally into the several orders included in the Gasteromyceteae. The Heterobasidiae show many points that set them apart from the Eubasidiae. Particularly is the gelatinous nature of the spore-fruits of the former noteworthy. The outer portion of the wall of the hyphae making up the spore-fruits possesses the property of swelling in water into a soft gelatinous mass, drying down again as the water evaporates. In these orders, too, the possession of clamp connections has not become as it were standardized, being found in some genera and absent in others. The orders Auriculariales and Tremellales are sometimes set apart from the other orders as the Phragmobasidiae, since the basidium is divided into four cells. The Dacryomycetales with forked but undivided basidia are then united with the remaining orders of the class under the name Holobasidiae. Gilbert has studied the nuclear behavior in these groups and find that in their essentials they are identical with those occurring in the Eubasidiae.

Order Auriculariales.—The fungi included in this order are some of them cosmopolitan but many are confined to the Tropics. They are largely saprophytes on wood. A few are true parasites, such as some species of *Eocronartium*, *Helicobasidium* and *Jola* occurring on mosses, *Septobasidium* (Figure 99), parasitizing upon scale insects, *Helicobasidium filicinum* on ferns, etc. According to Boedijn and Steinmann the East Indian species of *Helicobasidium* are parasitic upon roots. In *Helicobasidium* and *Phleogenia* (*Pilacre*) the mycelium shows clamp connections which seem not to have been observed generally elsewhere in this order. These are also found at intervals on the mycelium of *Jola* (*Cystobasidium*) *lasioboli*. The spore-fruits are external and vary from a more or less felt-like

film to a thin crust or to firm shelf-like structures standing out from the substratum. In *Phleogena* (Figure 100, A) they are upright and stipitate with an enlarged head. In size the spore-fruits vary from a few millimeters to several centimeters. When wet they are

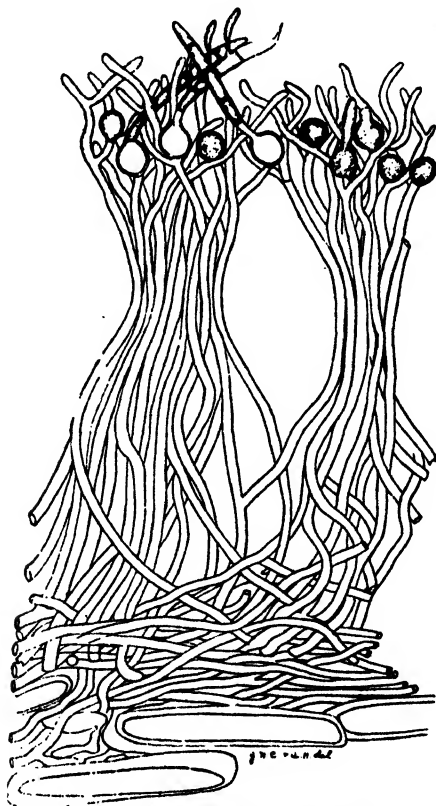


FIG. 99.—Auriculariales. *Septobasidium atropunctum*. (After Couch, 1929.)

mostly gelatinous (not so in *Septobasidium* and some other forms) drying down to a thin horny crust. The basidia are scattered here and there on the hyphal felt or are numerous in a sort of palisade, either in close contact or separated by paraphysis-like hyphae. The basidia are terminal to the hyphal branches but in *Jola* other basidia arise sympodially so that eventually the hypha has a somewhat zig-zag appearance with the basidia as apparently lateral structures on it. Each basidium arises as a somewhat enlarged

terminal cell of a dicaryon mycelium. The two nuclei unite and the basidium elongates somewhat, while the nucleus undergoes its two meiotic divisions (stichobasidial with reference to the axis of the spindle). In *Septobasidium* (Figure 99) and *Jola* there is first produced a rounded probasidium or hypobasidium in which the nuclear union occurs and out of which grows a short cylindrical hypha into which this diploid nucleus passes and undergoes its meiotic divisions. The hypobasidium may be somewhat thick-walled, thus increasing its resemblance to a teliospore. Even in *Septobasidium* in which the hypobasidium is usually formed it may, according to Boedijn and Steinmann, be lacking in some basidia. In the genera in which the basidia project above the surface of the spore-fruit the basidiospores are borne on relatively short sterigmata. On the other hand where the basidium is submerged in the gelatinous structure the sterigmata grow upward, parallel to the axis of the basidium, until they emerge, when they produce their spores. The basidiospores or the cells which may bud out from them give rise upon germination to a monocaryon mycelium which sooner or later becomes dicaryon in nature, but the method by which this is brought about has not been determined. Many of the species of this order produce conidia. For a few species microconidia are described which have not been brought to germination. It seems possible that these are male cells (sperms) but their function as such has not been demonstrated.

Ordinarily but one family is recognized, the AURICULARIACEAE, with twelve to fifteen genera and perhaps 100 or more species. Gäumann recognizes three families: Auriculariaceae with the simple type of basidium (i.e. without hypobasidium) and an external hymenium; Septobasidiaceae, with external hymenium and with basidia arising from a hypobasidium; Phleogenaceae, basidia without hypobasidium, enclosed in a loose hyphal peridium. Patouillard includes the Ustilaginales and Uredinales, as tribes of this family. The best known genera are *Auricularia* (Figure 94) growing on wood, with shelf-like gelatinous spore fruits several centimeters in diameter, smooth or reticulate on the hymenial (lower) surface, drying down to a scarcely noticeable hard crust; *Jola*, mostly parasitic on mosses, with less compact hymenium and with thin-walled hypobasidia; *Septobasidium* (Figure 99), parasitic on scale insects on bark, forming a rather close, non-gelatinous hymenium, the basidia with well

developed, sometimes thick-walled hypobasidium; *Phleogena* (*Pilacre*) forming small, stalked spore fruits 5 to 10 mm. tall, with rounded heads with an external zone (regarded by some mycologists as a sort of peridium) of radiating wavy hyphae at whose bases arise laterally the short basidia (Figure 100). The primary mycelium according to Shear and Dodge is without clamp connections and bears conidia; the dicaryon mycelium of the spore fruit bears the basidia but no conidia.

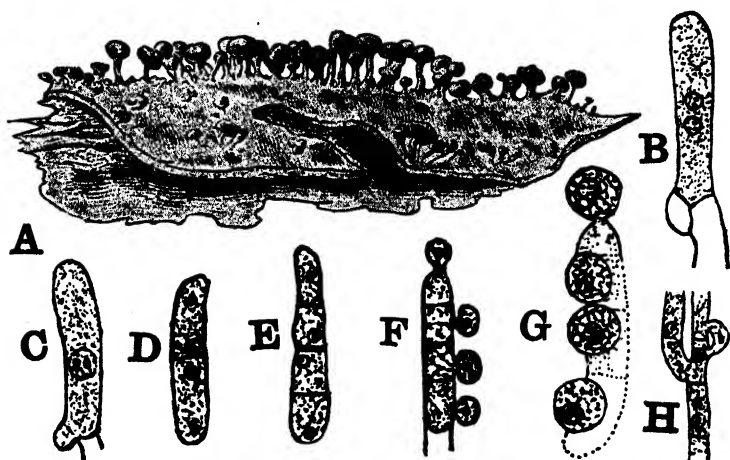


FIG. 100.—Auriculariales. *Phleogena faginea*. A, habit drawing; B-G, stages in the development of the basidium; H, portion of dicaryon mycelium with clamp connection. (A after Brefeld, 1888; B-H after Shear and Dodge in Jour. Agr. Res., 1925.)

Order Tremellales.—As in the foregoing group the species of this order are mostly saprophytic on wood. The majority of species are tropical but some extend to the cool temperate regions of the world, viz. *Tremella* (Figure 101), *Tremellodon*, etc. Clamp connections have not been reported in the mycelium and spore-fruits of most genera of this order. They are reported for *Sirobasidium sanguineum* and the author has observed them close to the hymenial layer in the spore-fruit of an unidentified species of *Tremella* and in *Exidia glandulosa*. In some species of the order the mycelium produces uninucleate conidia or oidia. Only as the spore-fruit approaches maturity do the dicaryon hyphae appear which produce the basidia. How the dicaryon condition arises is unknown, but the fact that in many cases a profuse production of uninucleate

oidia precedes this stage suggests that possibly the oidia are functional male cells and that, carried by insects, rain, etc., they fertilize the spore-fruits of opposite sexual phase as has been demonstrated for various other fungi. The spore-fruits vary from simple layers of basidia on the mycelium to structures of greater complexity—crusts, shelves, or even stalked *Hydnum*-like structures (*Tremello-don*). They are mostly gelatinous, drying down to inconspicuous

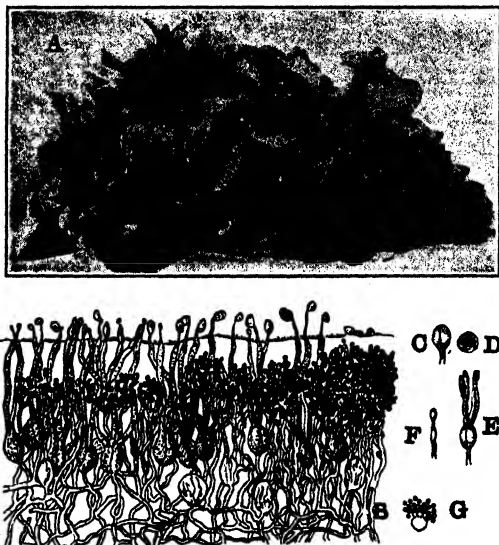


FIG. 101.—Tremellales. A, *Tremella frondosa*; B–G, *T. lutescens*. B, portion of hymenium; C–E, basidia of different ages and from different viewpoints; F, epibasidium, sterigma and young basidiospore; G, basidiospore germinating under water. (A after Atkinson, 1900; B–G after Brefeld, 1888.)

hard bodies. The basidia (Figure 101; C–F) are at first ovoid, enlarged, terminal cells of dicaryon hyphae. The nuclei unite and divide by meiotic divisions into four nuclei. Nuclear division is followed by the formation of a vertical septum, a second septum being formed at right angles to the first so that the basidium is divided into four longitudinal uninucleate quadrants. The position of the nuclear spindles is transverse so that the basidia are chiasmo-basidial. From each cell arises a slender epibasidium at whose apex a basidiospore is produced on a short sterigma. In the genus *Sirobasidium*, first studied by Lagerheim, the basidia are produced in chains, maturing successively from the apex downwards. These

basidia except for being in chains, are typical for the order in two species but in another species the septa are oblique, as occurs also in some cases in the genus *Tremella*. This has been considered by some mycologists to represent a transition from the Auriculariales to the Tremellales. In addition to the production of basidia many species produce conidia on various types of conidiophores.

The Tremellales may be divided into two families upon the basis of having the hymenium external (*Family Tremellaceae*) or enclosed (*Family Hyaloriaceae*). The genus *Sirobasidium* with basidia in chains is sometimes set apart in a separate family the *Sirobasidiaceae*.

FAMILY TREMELLACEAE.—In the tropical genus *Stypella* the fruit body is a small felty mass of tangled hyphae in whose upper layer the basidia arise. In *Sebacina* there is a more or less waxy crust with the hyphae of the upper portion directed perpendicularly to the surface, the terminal cells of these rather closely packed hyphae being the basidia. Cushion-like or lobed, gelatinous spore fruits are characteristic of *Exidia* and *Tremella*. These are distinguished by the occurrence of gland like dots in the spore-fruit of the former these being absent in the latter. The basidiospores of *Exidia* are mostly allantoid, those of *Tremella* straight and ellipsoidal to merely spherical (Figure 101, B, G). When these spores germinate the sprout-conidia of the former are mostly curved, those of the latter yeast-like. *Gyrocephalus* has funnel shaped spore-fruits with the hymenium on the outer surface only. In *Tremellodon* a stalked, light-colored, gelatinous pileus has on its lower surface numerous hymenium-covered teeth, resembling some species of *Hydnum*. *Tremella* is found in all parts of the world. *T. fuciformis* forms large white masses of gelatinous leaf-like lobes, the whole mass sometimes being 10 to 12 cm. in diameter. It is considered edible. Other species are usually smaller and some are bright colored.

FAMILY HYALORACEAE.—The single genus, *Hyaloria*, is tropical. The spore-fruits resemble small unopened mushrooms. At the top of the glass-like stipe a sort of head is formed by long tangled hyphae among which arise the basidia. These hyphae, as in *Phleogena*, form a sort of pseudoperidium.

The Tremellales must be considered as a group which has developed in a more or less close parallelism to the Auriculariales. The low, felty or gelatinous-waxy crust, bearing basidia on the upper surface, seems to be the most primitive in each order, and from this

simple structure have developed the more complex spore-fruit forms. It must be emphasized again that until the life histories have been more fully worked out the true relationships are only a matter of conjecture. The rather frequent occurrence of conidial production in these orders would hint a relationship to the Ascomyceteae in which conidia are produced abundantly.

Order Dacryomycetales.—Like the Auriculariales and Tremelales the species of this order are mostly saprophytic on wood. They

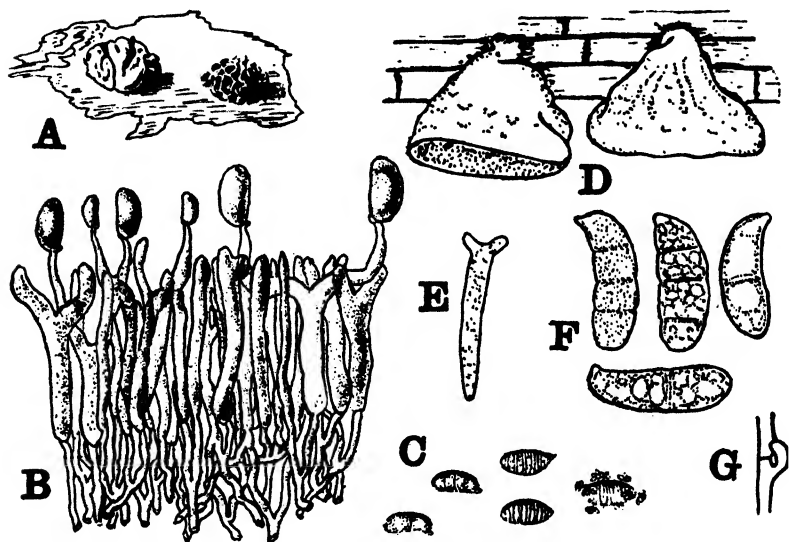


FIG. 102.—Dacryomycetales. A, *Dacryomyces lutescens*; B, portion of hymenium of *D. chrysocomus*; C, basidiospores of same in various stages of germination; D–G, *Heterotextus alpinus*. D, habit sketch; E, basidium; F, basidiospores; G, clamp connection. (A–C after Brefeld, 1888; D–G after Martin, 1932.)

occur both in the temperate and tropical regions of the world. Clamp connections have been observed by Martin in two genera of the order, viz. *Guepinia* and *Heterotextus* (Figure 102, G). The mycelium starts out as a monocaryon mycelium, which becomes changed to a dicaryon mycelium at the base of the spore-fruit, in a manner not yet discovered. The basidia arise from the dicaryon hyphae. Oidia or conidia are produced on the young spore-fruits. Dangeard has shown that in *Dacryomyces deliquescentis* these oidia are at first binucleate, arising from the dicaryon mycelium, but divide into two uninucleate oidia before germinating. The basidio-

spores often germinate by budding off minute uninucleate oidia. Whether either type of oidium has any sexual function is entirely unknown. The basidia are at first terminal binucleate cells in a sort of hymenial layer in the more or less gelatinous spore-fruit. The two nuclei unite and then divide meiotically in a stichobasidial manner until four nuclei are formed, two of which pass out into the two stout branches (epibasidia) the other two remaining in the body portion of the basidium (the hypobasidium) and degenerating. The epibasidia are of about the same diameter as the hypobasidium and often nearly as long. At the apex of each is produced, on a short sterigma, a single, usually ellipsoidal or more or less reniform basidiospore which quickly divides, by means of transverse septa, into two or more cells, even before separation from the sterigma (Figure 102, B, C, E, F).

But one family is recognized, FAMILY DACRYOMYCETACEAE, with 75 to 100 species in seven or more genera. As in the two preceding orders the spore-fruits vary greatly in complexity. They form a crusty structure, waxy in consistency, in *Ceracea*, and a gelatinous, cushion-shaped or more or less lobed and folded, bright-colored body in *Dacryomyces* (Figure 102, A). In *Dacryomitra* the spore-fruit is stalked, with a smooth or ridged head, often resembling a diminutive *Morchella*. *Calocera* is much branched and cartilaginous, and is often confused with *Clavaria*, from which it needs a study of the structure of the basidium to distinguish it. *Femsjonia* resembles a *Peziza*. All of these have the typical tuning-fork type of basidium.

Whether the gelatinous or waxy consistency of the spore-fruits, the abundant production of conidia and the tendency for the basidiospore to germinate by budding off small cells, characters common to the Auriculariales, Tremellales and Dacryomycetales, really indicate close relationship or not is a matter of uncertainty. In the author's opinion they are related and represent various evolutionary experiments in basidium formation among rather primitive Basidiomyceteae. Within each order the evolution of the fruit body has undergone more or less parallel development. All these orders are diverging twigs of a branch arising perhaps from somewhere near the Pezizales in the Ascomyceteae. From this same branch the highly specialized parasitic Teliosporeae probably took their origin. Somewhere on this branch, possibly near the Dacryomycetales, probably arose the Order Agaricales.

Studies by Juel, Neuhoff, Martin and Rogers have led the latter to an interpretation of the relationships in the class somewhat different from that in the foregoing paragraph. He holds, in common with some of the others mentioned, that the primitive basidium consisted of two parts, the basal hypobasidium, binucleate at first, within which the nuclear union occurs, and one or more outgrowths, the epibasidia. Into the latter the nuclei pass from the hypobasidium. Meiotic division may occur either in the latter or in the epibasidium, if there be but one. Each epibasidium produces a true sterigma which bears a basidiospore. The genus *Tulasnella* (Figure 103, C-E), often included in the genus *Corticium* of the Order Agaricales, is considered by Rogers to represent a primitive form. In the ovoid or pyriform hypobasidium of this genus the fusion nucleus divides into usually four nuclei. One of them passes out into each of the four (sometimes fewer) stout epibasidia which usually, but not in all species, become separated from the now almost empty hypobasidium by a basal septum. Each epibasidium produces a terminal sterigma and basidiospore. The nucleus may divide within the epibasidium and both nuclei pass into the basidiospore. By producing but two epibasidia, not separated by septa from the hypobasidium the typical tuning-fork basidium of the Dacryomycetales can be evolved. By crowding the basal septa down into the hypobasidium so as to divide that longitudinally into four cells the basidium of the Tremellales can be derived. By reduction of the size of the epibasidia until finally only the sterigmata are left, is developed the basidium characteristic of the Agaricales and most other Basidiomyceteae. Rogers attempts to explain the derivation of the hypobasidium and single, transversely septate epibasidium of *Septobasidium* of the Auriculariales and of the corresponding teliospore and promycelium of the Uredinales and Ustilaginales as being due to the delay in the meiotic division of the fusion nucleus until it passes out into an epibasidium which naturally would be single for a single nucleus. He believes that the hypobasidium of *Tulasnella* represents an ascus, perhaps of some form related to *Ascocorticium* (Order Taphrinales), in which the ascospores have pushed out into pockets, germinating there to form secondary spores. These pockets have become the epibasidia and the secondary spores have become the basidiospores.

On the other hand some students of these fungi consider the primitive basidium to have been of the holobasidium type from which the forked and septate types have been derived. The distinction of hypobasidium and epibasidium are, in this viewpoint, specializations to meet the need of holding the basidium over until a more favorable period. The thick walled hypobasidium (or "probasidium") such as is found in the Teliosporeae or in *Septobasidium* cannot, because of the thickened wall, develop in the manner normal for basidia, and so a thin-walled new structure, the epibasidium (or promycelium) was developed. The thickened apical branches of the basidia of the Tremellales and Dacryomycetales, and of *Tulasnella* are not considered to be epibasidia but merely modified sterigmata.

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CHAPTER XII

BASIDIOMYCETEA. AGARICALES (HYMENOMYCETEA)

Order Agaricales (Hymenomyceteae).—The 10,000 or more species making up this order are mainly saprophytic on wood but many live on organic matter in the soil. A few are true parasites on leaves, green stems, and fruits, and even on other fungi. The mycelium appears not to produce haustoria habitually even in the parasitic species, but they are present in *Exobasidium*. The production of clamp connections on the dicaryon mycelium is not universal, but is found in practically every family. To a much greater degree than in the fungi already studied the secondary mycelium (dicaryon phase) is of far greater importance in the life cycle, the primary mycelium (monocaryon phase) occupying but a short period of the life of the fungus. The dicaryon mycelium arises in many cases by the union of uninucleate mycelial cells or of oidia and mycelium, both of opposite sexual phase. The basidia are packed closely in a definite external hymenium, with few exceptions. Frequently a few larger sterile cells, cystidia, occur among the basidia but since these also arise from the dicaryon mycelium they are not homologous with the paraphyses of the Pezizales. The hymenium is exposed to the air at the time the basidiospores are shot off. In the forms considered by the author to be more primitive the hymenium is external from the first while in the more highly developed forms it is produced in the interior of the spore-fruits, becoming external only a short time before spore formation.

The basidia are mostly cylindrical or clavate (Figure 104), and one-celled, bearing at their outer end usually four basidiospores, on sterigmata varying in length according to the species. In some cases the basidium is short and ovoid, usually with long sterigmata (Figure 103, A). The two nuclei of the young basidium unite and then divide by meiotic division into four, each of which may pass into a basidiospore. Not rarely the nuclei divide once more before the spores are entered, four entering these and four remaining in the

basidium. Occasionally but two spores are formed, the two unused nuclei not passing into the spores, or two nuclei may pass into each of the two spores. In a few genera five or six or even more spores are formed on each basidium.

The most primitive type of spore-fruit consists of a crust on the surface of the substratum (*Corticium*). This may be reduced to a

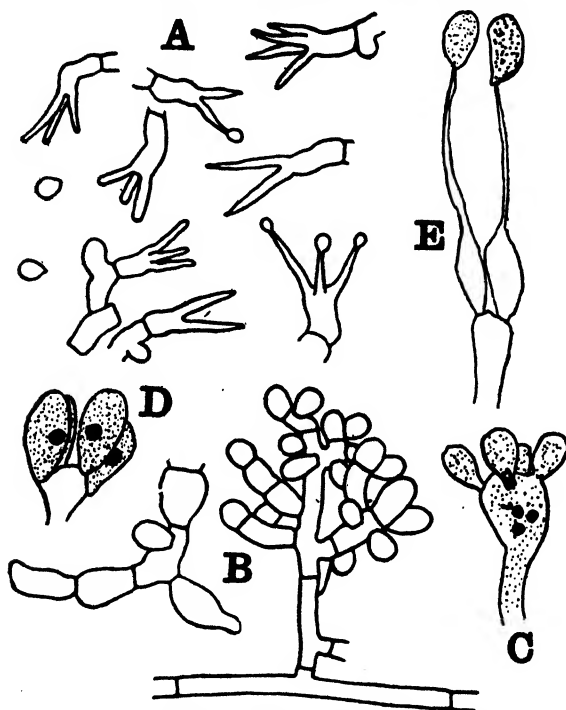


FIG. 103.—Agaricales, Thelephoraceae. A and B, *Corticium praticola*; C–E, *Tulasnella tulasnei*: C, hypobasidium with four epibasidia; D, the hypobasidium has emptied itself into the four epibasidia which have formed basal septa; E, two epibasidia, each with a long sterigma and basidiospore. (A and B after Kotila, 1929; C–E after Rogers, 1932.)

rather loose weft of hyphae with scattered tufts of basidia (*Hypoch-nus* and some species of *Corticium*, e.g. *C. vagum*) or to a hymenium of basidia formed between the epidermal cells of the host and breaking out through the leaf surface (*Exobasidium* Figure 104). From the crust type have arisen probably the shelf or bracket forms with smooth hymenium on the under surface progressing into forms in which the surface is thrown into folds, pits or teeth to increase the

hymenial surface. In many the spore-fruit produces a central stalk (stipe) and a more or less circular head (pileus). Other forms are club-like or ramosely divided. In consistency the spore-fruit may be felty, papery, corky, woody, fleshy or more rarely gelatinous. In some cases by autodigestion of the hyphae the spore-fruit dissolves progressively into a liquid (*Coprinus*). The size varies from a few millimeters up to several decimeters in diameter. The spore-fruit may be evanescent or may be perennial and last many years. The range of color is very great; white, gray, yellow, orange, brown, red, green, blue, etc. The basidiospores are one celled, but in a few cases become septate before germinating (*Exobasidium*). They are more often hyaline but are colored in many genera. They usually germinate directly by a germ tube. Conidia are produced on various types of conidiophores; especially in the families first to be considered and which are possibly the more primitive from an evolutionary standpoint.

The author follows the more usual custom and divides the order into seven families. Some specialists in this group subdivide some of these families (e.g. Agaricaceae) so as to recognize 12 to 15 in all.

FAMILY THELEPHORACEAE.—Hymenial surface smooth or at most only slightly warty or folded. Spore-fruits membranous, leathery, or in two or more genera fleshy; closely appressed to the substratum or forming a shelf or funnel or simple or divided pileus with hymenium on one surface only. Twenty or more genera are recognized and probably about 1000 species. The most complete study of the North American species of this family is that by E. A. Burt.

The genus *Corticium* forms a thin spore-fruit growing closely appressed to the substratum and not distinguishable into several layers. The hymenium arises directly from the mycelium (Figure 103, A, B) and consists of a layer of closely packed basidia (in a few species they are scattered or in loose tufts, e.g. *C. vagum*). The margin of the spore fruit may be definite or indefinite. When dry the hymenium is often cracked. There are no cystidia among the basidia. The color of the hymenium is prevailingly some shade of gray but other colors may be present instead. *C. vagum* is parasitic upon stems and roots of potato (*Solanum tuberosum*), bean (*Phaseolus vulgaris*) and many other plants of economic value. It produces cankers at or below the surface of the soil which kill or seriously injure the parts affected. Small sclerotia are formed which

enable the fungus to overwinter. On the stem of the host plant the mycelium creeps up as a thin hyphal layer on which the oval basidia are produced in groups. The sclerotial stage is known under the name of *Rhizoctonia*. Most of the species of *Corticium* are saprophytic on wood and bark and form spore-fruits with definite margin. Closely related to this genus are *Hypochnus* and one or two other genera often united with it into a separate family. They have a more or less cottony mycelium (with clamp connections) on which arise tufts of basidia much as in *Corticium vagum*. The basidiospores are spherical and spiny. They are mostly saprophytic on bark, leaves, etc. The presence of sharp-pointed cystidia far overtopping the surrounding basidia distinguishes *Peniophora* from *Corticium*. In *Aleurodiscus* the spore-fruit is disk or saucer shaped and paraphysis-like structures are intermingled with the basidia. In *Stereum* the spore-fruit is in three layers. While a few species are resupinate as in *Corticium*, many are shelf like or even laterally stalked, with a definite pileus. The hymenium is smooth, without projecting cystidia, but in some cases with paraphysis like cells. *Hymenochaete* differs from *Stereum* in the presence of brown cystidia visible under a hand lens. In *Thelephora* the spore-fruit is leathery and upright with a single or branched stalk spreading out into a fan-like or funnel shaped pileus, with the hymenium on the under or outer surface. The hymenium is smooth or with low ribs or slightly warty. *Craterellus* is also mostly more or less funnel shaped but is thicker and more fleshy, often bright colored. The external hymenium may be smooth or with more or less branched longitudinal ridges. *Cyphella* resembles a small cup or funnel with the hymenium on its inner surface. Some species are apparently parasitic upon mosses. *Solenia* is recognized by its cylindrical, tubular spore-fruits with the hymenium lining the inner surface, and with the individual fruits separate or pressed together so as to form a coherent body several millimeters high and of varying diameter.

The genus *Tulasnella* (Figure 103, C-E), discussed in the preceding chapter may find a place in this family for the time being. Its spore-fruit is a thin web of hyphae bearing the somewhat scattered basidia, much as in some species of *Corticium* and *Hypochnus*. It is waxy or mucilaginous. The hypobasidium, to follow Rogers' view of the basidial structure, is ovoid or spherical, with at first two nuclei. After fusion these divide meiotically and pass out into the

(usually) four apical, spore-like epibasidia which may become separated from the now empty hybobasidium by septa. From each epibasidium a basidiospore arises on a slender sterigma. Sometimes the epibasidium falls away from the hypobasidium before the production of its basidiospore. The justification of the retention of the genus within this family lies in the fact that some species of *Corticium* have rather long sterigmata which are enlarged in the

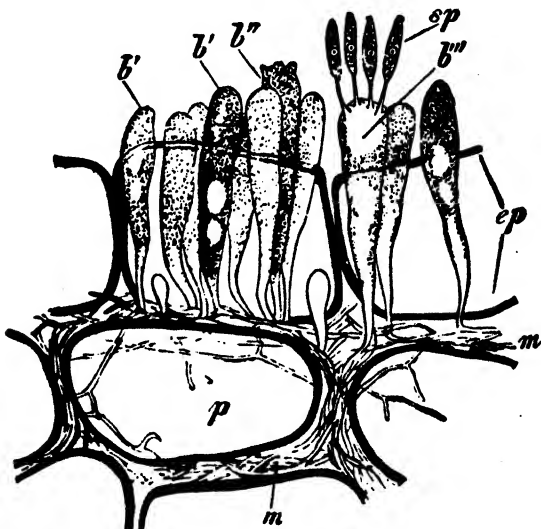


FIG. 104.—Agaricales, Exobasidiaceae. *Exobasidium vaccinii*. (After Woronin, 1867.)

basal portion so that they resemble the epibasidia of *Tulasnella*. In one species of the latter, *T. anceps*, the epibasidia are not separated by septa from the hypobasidium, but in other characteristics it is like the remaining species of *Tulasnella*. It is evident that the nuclear behavior within the true *Corticium* species needs further study to determine whether *Corticium* and *Tulasnella* are really closed allied.

FAMILY EXOBASIDIACEAE.—The fungi composing this family are parasitic in the leaves, green stems or even fruits of higher plants, often distorting the affected parts or causing the formation of galls. The intercellular mycelium apparently bears no clamp connections. It sends rod shaped or branched haustoria into the host cells. The basidia arise singly or in tufts between the epidermal cells (Figure

104), eventually piercing the cuticle and forming their 4 to 6 to 8 spores externally. There are no paraphyses or cystidia. Eftimiu and Kharbush have made an extensive study of *Exobasidium*. The mycelial cells within the host are elongated but become shorter nearer the epidermis and binucleate. The fusion nucleus divides meiotically into four nuclei, one passing into each basidiospore or one nucleus may degenerate and the remaining three divide, the six nuclei passing out into six spores. Sometimes only two nuclei are found in the basidium and then only two basidiospores. The spore germinates by budding like yeasts, except in *E. rhododendri* in which the spores divide by a septum and send out germ tubes from each of the two cells thus formed. In the same species the nuclear division within the basidium may be stichobasidial or chiastobasidial. About 30 species are known and perhaps 5 or 6 genera. *Exobasidium vaccinii* is frequent upon the cranberry (*Oxycoccus macrocarpus*) and related plants. The affected shoots become upright and take on a pink color. The leaves are sometimes increased in size and the stem is thickened. Sometimes only a small portion of a leaf may be infected. Such a spot is thickened and reddened. The basidia are club-shaped with 4 basidiospores which become septate before germination and send out short branching sterigmata with spindle-shaped spores. *Microstroma juglandis* causes white patches on the under side of the leaves of *Juglans* and *Hicoria*. The cylindrical basidia emerge in tufts from the stomata and bear usually six spores. In this connection it must be noted that Wolf's cytological studies of this fungus convince him that it is not a Basidiomycete at all, because its "basidia" are multinuclear, the mycelium lacks conjugate nuclei and the spores are not borne upon the sterigmata in the manner typical of the class. He believes that it should be assigned to a position among the Fungi Imperfecti. It seems probable that the true Exobasidiaceae are related closely to the parasitic *Corticium* species in the preceding family.

FAMILY CLAVARIACEAE.—Spore-fruits fleshy or waxy or even gelatinous, rarely leathery; upright, clavate or branched in a coralloid manner; round or flattened; covered by the hymenium on all sides. Eight or more genera and probably 400 to 500 species. All are saprophytic or possibly some form mycorrhiza on tree roots. Many of the larger forms are edible. The family appears to be derivable from the Thelephoraceae from which it differs in the more

fleshy consistency and the development of the hymenium on all sides.

Pistillaria with two-spored basidia and *Typhula* with four-spored basidia, with the spore-fruits often arising from a small sclerotium, are small slender fungi, often only a few millimeters tall, frequently with a thread like stalk. The fleshy hymenium-bearing portion is



FIG. 105.—Agaricales, Clavariaceae. *Clavaria pistillaris*. (After Coker, 1923.)

clavate or spindle shaped or cylindrical. *Clavaria* is large, growing on the ground or on rotten wood. It may be simple, forming a club-shaped structure up to 10 cm. tall and 2 to 3 cm. thick (*C. pistillaris*, Figure 105) or is more often branched in a coral-like manner (Figure 106). The branches are round and covered by basidia on all sides. The species are of various colors. *Sparassis* is fleshy and much branched into leaf-like structures. It forms a more or less spherical, bushy body 5 to 40 cm. in diameter and is edible. Cotton claims that the hymenium occurs only on the lower side of these "leaves," hence the fungus should be considered as belonging to the Thelephoraceae, rather than to the Clavariaceae.

FAMILY HYDNACEAE.—These fungi are mostly saprophytic. Some cause serious decay of timber. The fruit body is well developed;

resupinate, shelf-like, or with a pileus borne on a lateral or central stipe. In some forms the pileus is divided up into many small pilei. The consistency varies from fleshy to woody and there is a great range of color. The under side of the fruit body is at first smooth but as the hymenium develops it grows out into hymenium-covered spines or teeth. In some of the fleshy species (*Hericium caput-ursi*, *H. coralloides*, etc. Figure 107) the pileus is but little developed, the fruit body consisting essentially of branching stalks

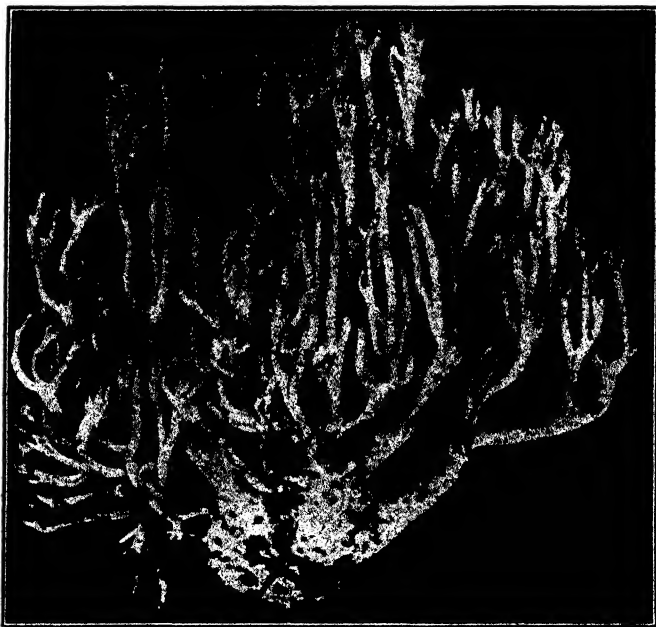


FIG. 106.—Agaricales, Clavariaceae. *Clavaria subbotrytis*. (After Coker, 1923.)

bearing terminally pendent tufts of long pointed, fleshy teeth. It is to be questioned whether such structures are true Hydnaceae at all or perhaps more closely related to *Clavaria* and *Sparassis*. In some forms with flattened teeth the young smooth hymenial surface first develops ridges to form shallow pores (as in the Family Polyporaceae) and at certain points on the edges of these circular ridges the growth becomes more active, producing flattened teeth connected at their bases into a shallow pore. Such forms (*Irpex*) have been placed by some mycologists in the Polyporaceae. The 500 to 600 species of Hydnaceae are placed in 10 to 15 genera. The

chief genus is *Hydnum* with about 150 species. These have round teeth. In addition to the fleshy forms of this genus there are some species that are more or less corky, with shelf like or centrally stipitate pileus. Some of the more recent authors, Coker, Banker and Miller subdivide the genus *Hydnum* into several genera. The fleshy species mentioned above, with much branched stipe and

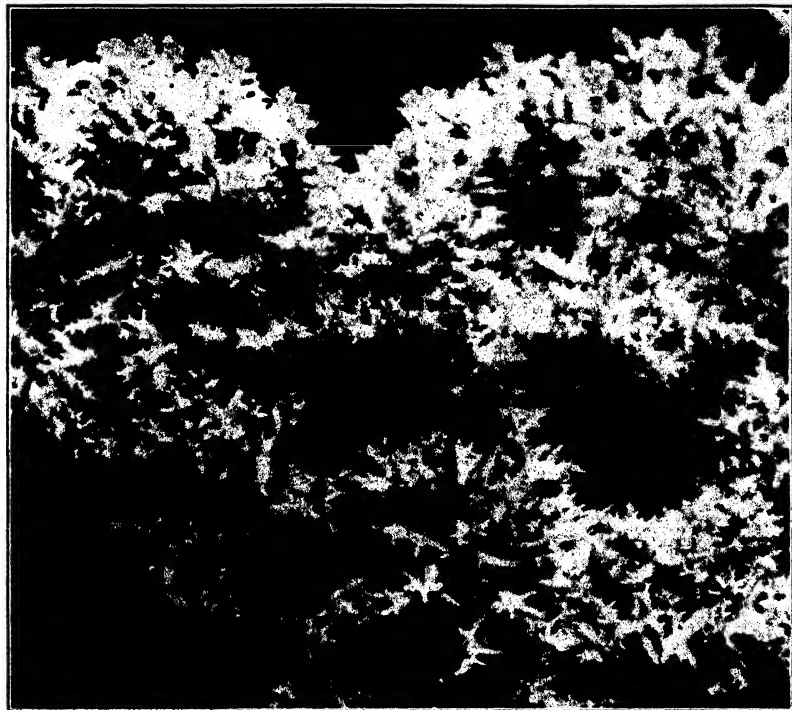


FIG. 107.—Agaricales, Hydnaceae. *Heridium* (*Hydnum*) *coralloides*. (Original.)

pileus fall into the genus *Heridium* (or *Manina*). *Irpex* is resupinate and has flattened teeth. Other resupinate forms (*Radulum*) have low warty projections instead of well developed teeth. They form a transition from the forms like *Corticium* and the resupinate *Stereum* species. *Echinodontium*, causing the decay of the wood of *Tsuga* on the Pacific Coast of North America, was formerly used by the Indians as a source of pigment as its rather large, corky or almost woody spore-fruits are bright colored.

FAMILY POLYPORACEAE.—In the sense that the cells invaded by the fungi of this family are mostly no longer living, i.e. wood fibres and tracheary tissue, these fungi are saprophytes. Many of them, however, attack only the sap wood of living trees, in which living cells are intermingled with the dead fibre and tracheary cells, bringing about a "sap rot" and death of the tree. Others, though confined to the heart wood which contains few if any living cells, attack this only in living standing trees. Still others only attack the wood of dead trees or of structural timbers, etc. So there are all grades of practical parasitism even though the particular cells invaded are not living. A very few species of this family are directly parasitic upon other fungi. Although most species are wood inhabiting some grow on the ground, obtaining their nourishment from buried pieces of wood or from the vegetable matter in the soil. Such species are true saprophytes.

The spore-fruits may be fleshy or fleshy-leathery when young but at maturity are, with few exceptions, papery, leathery, corky or even woody. They range in size from a few millimeters in width and one or two millimeters in thickness to a width of 75 cm. (specimens of *Fomes applanatus* collected by the author) and 30 to 50 cm. thick (specimens of *Fomes laricis* seen by the author). They may be evanescent or may live many years; according to Atkinson over 80 years in the case of specimens of *Fomes igniarius*.

The spore-fruits may be closely appressed to the under side of tree branches, logs, boards, etc., without a free margin, or may grow out laterally like a shelf or bracket, or may be stalked laterally or centrally. The under side is usually smooth when young, as in the Thelephoraceae, but develops unevenly so as to leave numerous pits (the pores) of various shapes on whose inner face the hymenium develops (Figure 108, A, B). With but few exceptions the pores are directed downward so that as the spores are shot off from the sterigmata of the basidia that line the pore they drop down and out of the pore into the open air where they are carried off by currents of air. In *Merulius lacrymans* (Figure 109) the pore-bearing surface may occupy any position with reference to the direction of gravity, the very low pore walls permitting air currents to reach the spores within the pores themselves. In this species the hymenium covers the bottom, sides and edges of the pores while in most cases it is the sides of the pores or sometimes the bottom (really the

upper closed end of the pore) but not the edges that produce the hymenium. In some species conidiophores are produced on the spore-fruit and give rise to numerous conidia.

The vegetative mycelium is slender and branching, the individual cells often being rather long. In some species of *Merulius* long mycelial strands are formed containing internally conducting and storage hyphae surrounded by protective hyphae. These strands

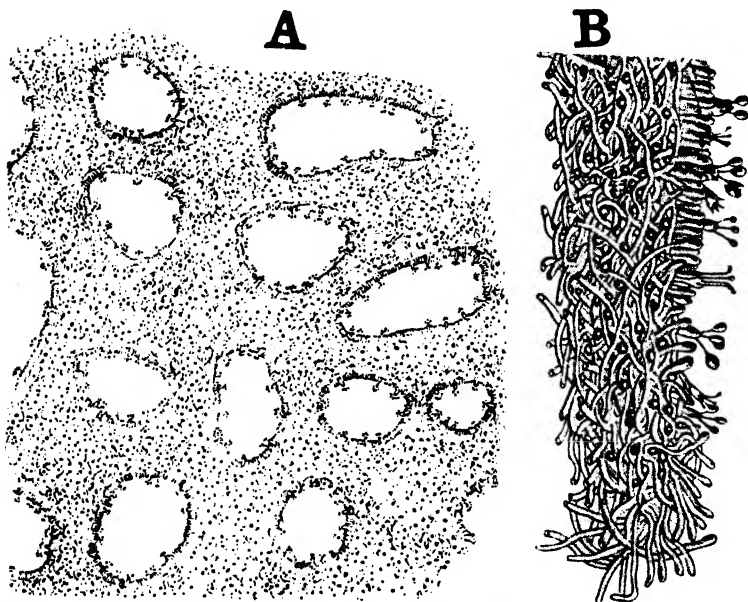


FIG. 108.—Agaricales, Polyporaceae. *Fomes annosus*. A, cross section of several pores; B, longitudinal section of a pore near its mouth. (After Brefeld, 1889.)

are able to creep through cracks in a wall for long distances until another favorably situated body of wood is found upon which the fungus begins its activities. Some species of *Polyporus* produce large tuber-like, subterranean sclerotia the size of a man's head (e.g. *Pachyma cocos*). From these the spore-fruits arise when conditions are favorable.

The process of sexual reproduction is unknown in the family. The mycelium of the spore-fruits appears in most cases that have been studied as to this point to have clamp connections as does to a large degree the vegetative mycelium growing in the wood. The

basidia eventually have four or eight nuclei, four of which pass into the four basidiospores whose nuclei in some cases divide so that the spores become binucleate. In some species the mycelium shows by the presence of clamp connections that it is secondary or dicaryon in nature immediately after germination. In such species the single nucleus of the basidiospore divides into two before the spore is set free. Apparently this is the source of the nuclear pairs in these species. Whether in the "heterothallic" species two primary mycelia of opposite sexual phase must meet and unite, or whether oidia may function as male cells to "diploidize" the primary mycelium still awaits investigation.

The number of species is very uncertain. Several thousand have been described but it is certain that very many of these are synonymous. The opinions as to the validity of described species vary greatly. Thus in Gäumann-Dodge, *Comparative Morphology of Fungi*, the genus *Polystictus* is credited with nearly 1000 species while Killermann in the second edition of Engler and Prantl, *Die Natürlichen Pflanzenfamilien*, admits only "some hundreds." The agreement is still less as to generic limits. Killermann recognizes 17 genera in the family limits adopted in this work, but Murrill, in the *North American Flora* recognizes 78 genera for North America alone, aside from *Merulius* which he excludes from the family. Perhaps on a very conservative basis one may estimate 2000 to 2500 species in the family.

In the following discussion of the more important genera of Polyporaceae these have been retained, in the main, with the older generic limits although in the author's opinion that is too conservative. Further life history and anatomical studies such as that of Miss Ames should enable us to establish more rational bases for distinguishing the genera. In parenthesis after each name are placed some of the more important segregates recognized by Karsten, Murrill and others.

Merulius is a genus of wood-destroying fungi with wide spreading low spore-fruits on the surface (not always the lower surface) of the wood or adjacent soil. At first this has a smooth hymenial surface on which some basidia come to maturity but soon it is thrown into low folds or ridges in several directions, resulting in the formation of shallow pits of various shapes with basidia of different ages covering the bottoms and sides of the pits and the edges of the low inter-

vening ridges. Clamp connections are numerous on the mycelium. The best known species is *M. lacrymans*, (or *M. domesticus*, according to Falck, Figure 109) which is very destructive to woodwork in buildings. Because of the origin of the hymenium as a flat surface which later is thrown into folds and irregular reticulations with

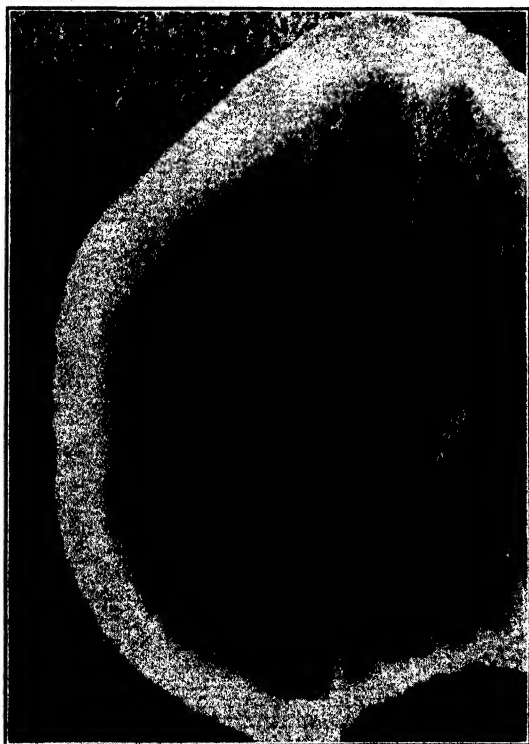


FIG. 109.—Agaricales, Polyporaceae. *Merulius lacrymans* (*M. domesticus*).
(After Falck, 1912.)

basidia on the edges of the ridges this genus has been excluded from the Polyporaceae by some authors and placed in a separate family or even relegated to the Hydnaceae. *Poria* (Figure 110) produces resupinate spore-fruits which adhere to the substratum and consist mainly of a thin layer of underlying mycelium and the pore layer. Some species produce their fruiting bodies only on the under side of branches or logs so that the pores point directly downward but this is not the case in all species. The pores are mostly rather

small, angular or round, and not very deep. The spore-fruits vary in size and color as well as in color of the spores. Some species are destructive to woodwork. It is certain that many species assigned to this genus are only resupinate forms of other genera such as *Polyporus*, *Fomes*, *Trametes*, etc. *Polyporus* (*Bjerkandera*, *Rigidiporus*, *Piptoporus*, *Inonotus*, *Spongipellis*, *Laetiporus*, *Grifola*, *Phaeolus*, etc.) produces spore-fruits which grow out from the

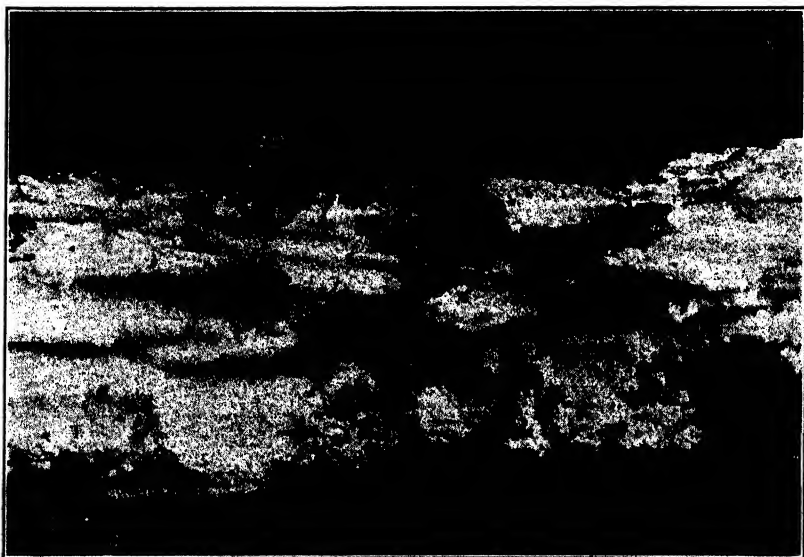


FIG. 110.—Agaricales, Polyporaceae. *Poria albolutescens*. (Original, Dow V. Baxter.)

substratum like a shelf or are stalked laterally or centrally. The young spore-fruits are fleshy but toward maturity they become hardened so as to be corky or soft woody. The pore layer is quite different from the remainder of the spore-fruit and can usually be separated from it. The upper surface of the pileus as well as the pore layer may be of various colors. The spores are mostly hyaline. Among the larger species is *P. sulphureus* (*Laetiporus speciosus*), which forms a series of shelves up to 60 cm. broad, bright-yellow to orange in color and rather fleshy and edible at first and dry and cheesy at maturity. It occurs at the base or on the trunk of deciduous trees (Figure 111), often oak (*Quercus*), whose wood it destroys. *Polyporus elegans* has a light brown pileus several centimeters in

diameter supported by an almost central dark colored stipe. It grows on fallen wood. *Polyporus (Pycnoporus) cinnabarinus* forms its laterally attached shelves, 5 to 10 cm. wide and up to 1 cm. thick, on the sides of trees. The bright cinnamon-red color makes it very attractive. It is rather corky or punky at maturity. *Polystictus (Mucronoporus, Coriolus, Corioloopsis, Inoderma, Coltricia, etc.)* produces spore fruits that when mature are membranous or leathery and usually thinner than those of *Polyporus*. They are also laterally

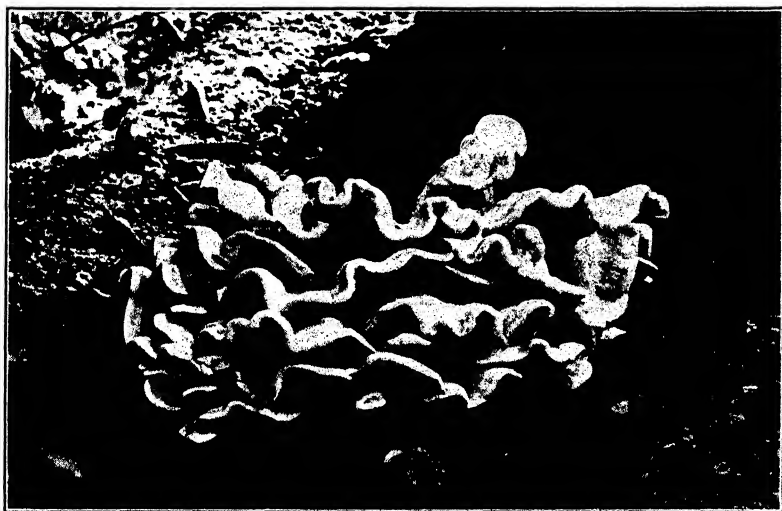


FIG. 111.—Agaricales, Polyporaceae. *Polyporus sulphureus*. (Original, F. C. Strong.)

attached like shelves or brackets or less often laterally or centrally stalked. Frequently the upper surface is zonate, smooth or hairy. The pores are usually not very deep and the tissues of the pore walls are continuous with the tissues of the pileus. Many species produce spore-fruits crowded above one another in tiers, or imbricated. On the under side of tree limbs they are resupinate as in *Poria* and some species of *Polyporus*, but form shelves at the edges. The same species may be resupinate on the under side of a log, shelf-like along its sides and short stalked or funnel-shaped on the upper side. *Polystictus (Coriolus) versicolor* is very common on dead stumps, logs, etc. It forms great numbers of overlapping semicircular or kidney-shaped, velvety-haired pilei which are strongly marked by

zones of various colors. The individual pilei are 2 to 5 cm. in diameter. In *P. (Coriolus) abietinus* the pores at maturity break up into flattened teeth. The upper surface of the pileus is grayish-white and hairy, the pore surface violet colored in fresh specimens. The spore-fruits are formed on branches, logs, etc., being resupinate on the under side but forming shelves at the edges. *Polystictus (Coltricia) perennis* grows on the ground in forests. It has a funnel-shaped spore-fruit with a central stem. *Cryptoporus* is a genus of but one recognized species, *C. volvatus*, which grows on coniferous wood throughout the northern part of the United States and in Canada and in Japan as well. It differs from *Polyporus* in being closed at first by a thick veil which gradually ruptures leaving an opening to the cavity into which the pores open. The formation of a veil covering the hymenial portion of the spore-fruit is unknown in other genera of this family. *Trametes* is described with the supposedly diagnostic character that the tissues of the pore layer are not distinguishable nor separable from those of the remainder of the spore-fruit. The pores may be sunk to different depths into the pileus tissue. The body of the pileus is corky or punky, rarely woody, mostly with only one layer of pores, rarely with several layers representing several growing seasons. The distinction between *Trametes* and *Fomes*, *Polyporus*, etc. is clear in some species but difficult to make in others. As a result a great lack of agreement exists as to the limits of the genus and as to the species to be included. Most of the species segregated in the genera *Coriolellus*, *Porodaedalea* and *Pogonomyces* as well as some of the species of *Polyporus*, *Fomes*, *Polystictus*, etc., have been included at some time in *Trametes*. It is, indeed, not at all certain that the characters mentioned above serve to bring together species that are really congeneric. More likely they are variations that may arise within several different genera. Murrill recognizes as properly belonging to *Trametes* only 8 species in North America, mostly subtropical or tropical. *T. suaveolens* on decaying willow trunks is the type species of the genus as so delimited. *Fomes* is another genus which has been segregated into many genera (*Ganoderma*, *Amauroderma*, *Fomitella*, *Pyropolyporus*, *Nigroporus*, *Globifomes*, *Elfvigia*, etc.). The chief character common to all is the perennial nature of the spore-fruit which produces successive layers of pores in succeeding growing seasons (Figure 113). The spore-fruits are usually punky or woody. The

species with the upper surface of the punky or corky spore-fruit covered by a reddish brown varnish may well be set apart as a separate genus *Ganoderma*, of which *G. tsugae* is very common in the United States on decaying trunks and roots of the hemlock (*Tsuga*). Its fruiting bodies are fan shaped from a thick lateral stipe. *G. curtisii* is very similar but grows on deciduous trees, also in the



FIG. 112.—Agaricales, Polyporaceae. *Fomes applanatus*, habit view on maple. (Original, F. C. Strong.)

United States. Some species of *Ganoderma* are never perennial in habit, producing but one layer of pores. *Fomes laricis* (*F. officinalis*) was formerly used for medicinal purposes. Its spore-fruits grow on the larch (*Larix*) and other Conifers and sometimes attain a diameter of 15 cm. and a height of 40 to 50 cm., with very many layers of pores. *F. unguatus* (*F. pinicola*) causes the decay of pines and other standing trees. *Fomes* (*Pyropolyporus*) *igniarius* forms hoof-like spore-fruits on standing oak (*Quercus*) and other deciduous trees whose wood it decays. *Fomes* (*Elfvigia*) *fomen-*

tarius forms somewhat similar fruiting bodies with a hard crust-like, upper layer, on standing trees. *Fomes applanatus* (*Elfvigia megaloma*) is one of the commonest species in North America, being found on fallen trees and old stumps almost everywhere (Figures 112, 113). Its spore-fruits are gray above, with a definite crust, and may attain a diameter of 75 cm. White estimates that a large spore-fruit of this species may liberate 30,000,000,000 spores a day for several months attaining a total of 5,500,000,000,000 spores for the

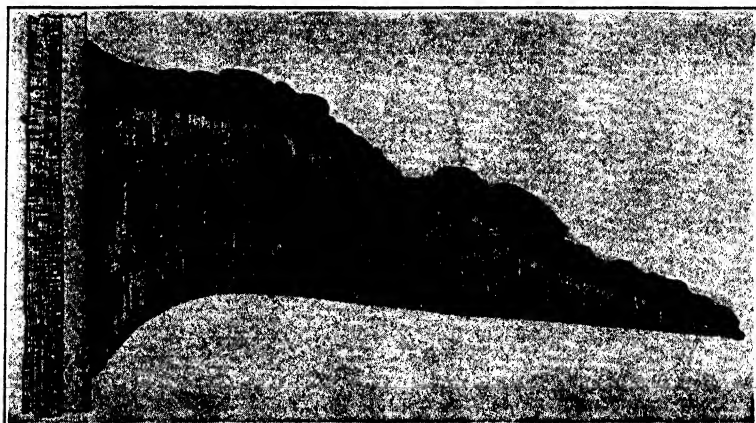


FIG. 113.—Agaricales, Polyporaceae. *Fomes applanatus*; vertical section through three year old sporophore. (After Buller, 1909.)

season. Yet of all this vast number of spores carried far and wide by the wind all but a very few must perish. With so many spores in the air it is not to be wondered at that the fungus is very common wherever a deciduous tree has died or its trunk has fallen, for this fungus does not attack healthy, uninjured trees. *Daedalea* is distinguished by having the pores elongated or labyrinthiform. Its spore-fruits are shelf-like and corky. *D. confragosa* is very common in North America and Europe. In *Lenzites* the pores are elongated radially from the point of attachment so as to resemble gills, with occasional cross connections which may disappear with age. The spore-fruit is more or less corky. *L. betulinus* is common on birch (*Betula*) and other trees in North America and northern Eurasia. Its fruiting bodies are 3 to 7 cm. broad, 3 to 10 mm. thick, velvety and zonate above. But for the cross connections of the young specimens this might well be placed in the Family Agaricaceae.

The course of evolution within the family is very uncertain. It seems likely that the resupinate forms like *Poria* are more primitive and that from these have arisen the genera known collectively as *Polystictus* and *Polyporus*. From the latter have probably developed *Trametes*, *Fomes*, *Daedalea* and *Lenzites*. Whether *Poria* arose from *Corticium*-like fungi in the Thelephoraceae or from some of the Hydnaceae with teeth becoming connected at their bases to form shallow pores is unsettled. Possibly the Family Polyporaceae is not monophyletic but arose from both Thelephoraceae and Hydnaceae.

FAMILY BOLETACEAE.—This family consists of fungi growing on the ground almost exclusively. The spore-fruits are fleshy and stipitate, centrally so in most species. The pileus is thick and convex and the layer of pores is easily separable from it. The pores are easily broken apart from each other. In some genera a veil covers the layer of pores in the young spore-fruits, extending from the edge of the pileus to the stipe. As the pileus expands the veil tears loose from its edge and remains as an annulus on the stipe. In two genera the pores are elongated somewhat in a radial direction, suggesting a transition to or from the Agaricaceae. Some of the species are large, with pileus up to 40 cm. broad and 4 to 6 cm. thick. The spore layer may grow up to the stipe and be attached to it or may be free from the stipe. The flesh of many species becomes blue when bruised, in others it does not change color. Some species are edible, some are known to be poisonous. About a dozen genera are recognized with over 200 species, of which Murrill describes 75 in North America and the adjacent West Indies. *Tylopilus* with flesh-colored spores and reticulated stipe without veil or annulus is represented commonly in North America and Europe by *T. felleus* (Figure 114) which is usually 10 to 15, sometimes up to 40 cm. broad. The surface is smooth and chestnut brown and the white interior flesh is bitter. *Ceromyces crassus* (*Boletus edulis*) is also found in North America and Europe. It averages larger, 6 to 20 cm. broad and 2 to 4 cm. thick. Its spores are brown in color. The stipe is more or less reticulated. The pileus is reddish brown, white or yellowish within and somewhat glutinous externally. The yellowish pores become greenish with age. This species is much prized for food in Europe. *Suillellus* has yellowish pores with red mouths. In *S. luridus* (*Boletus satanas*) the pileus is 5 to 12 cm. broad, reddish or yellowish brown, with the white flesh turning blue

when bruised. The stipe is red below and yellowish above, and covered with red dots. It is considered poisonous. *Boletus*, in the limited sense, has a smooth, viscid pileus and the young tubes are covered by a broad veil which becomes an annulus. *B. luteus* with dotted, yellow or reddish stipe, very viscid yellowish brown to reddish brown pileus and honey-colored pores, is common in moist deciduous forests and edible. *Strobilomyces* has black spores and a blackish, shaggy pileus and stipe, the pores at first covered by a



FIG. 114.—Agaricales, Boletaceae. *Tylopilus (Boletus) felleus*. (After Atkinson, 1900.)

veil. *S. strobilaceus* is not rare, edible. *Boletinellus merulioides* with its excentric or lateral stem and pores "formed by radiating lamellae 2-3 mm. apart, branching and connected by numerous irregular veins of less prominence" (Murrill) approaches closely to some species assigned to the genus *Paxillus* in the Agaricaceae.

FAMILY FISTULINACEAE.—This small family of only a few species and two, possibly more, genera, is distinguished by its fleshy spore-fruits and by the separate (though closely crowded) hollow tubes which hang down underneath the pileus. The latter may be laterally or centrally stipitate in *Fistulina* or resupinate in other genera. Each separate tube is closed at first but opens at maturity and is lined internally by the hymenium. If one would imagine hundreds

of spore-fruits of *Solenia* (of the Thelephoraceae) arising from a common pileus the characteristic structure of this family would be realized. *Fistulina hepatica*, the beefsteak fungus, is found in nearly all temperate regions of the world on oaks and other deciduous trees. The spore-fruit is more or less fan shaped with a short thick lateral stipe. It is brown-red, blood-red internally, and the closely crowded but separate tubes are reddish brown. When young it is edible. The relationship of this family to the Polyporaceae is

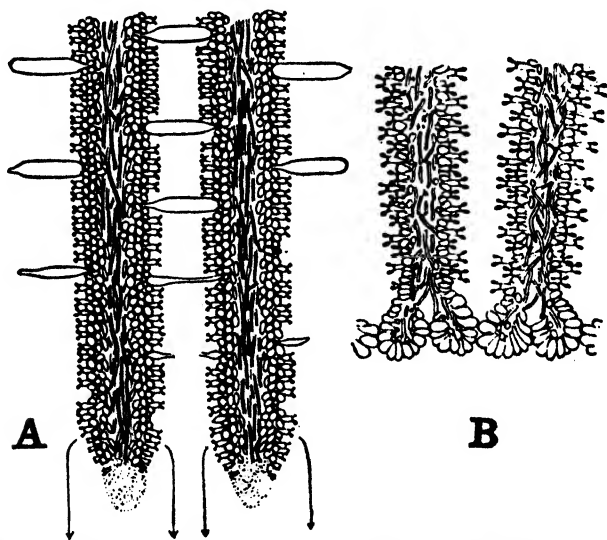


FIG. 115.—Agaricales, Agaricaceae. A, *Coprinus atramentarius*, section of two gills showing cystidia. Autolysis is beginning at edge; B, *C. sterquilinus*, section of gills showing thickened edge to hold gills apart. Note long and short basidia. (After Buller, 1910.)

doubtful. The easily separable pores of some of the Boletaceae suggest a possible relationship to that family. The similarity to a compound *Solenia* has been mentioned.

FAMILY AGARICACEAE.—This is the largest family and is probably to be regarded as the culmination of the evolutionary development within the Order Agaricales. Between 5000 and 6000 species are recognized at a very conservative estimate. As is to be expected in a large culminating evolutionary group, the extremes of variation are very great. The characteristic feature of the family is the production of radiating lamellae (gills) which are entirely covered

or all but the edge, with the hymenium (Figure 115). This may or may not extend from gill to gill on the interlamellar surface of the pileus. The interior tissues of the lamella (the trama) may continue unchanged up into the pileus or the pilear tissue may be distinct in structure, color etc. from the tramal tissue, paralleling the conditions mentioned in the Polyporaceae.

In contrast with the Polyporaceae where the spore-fruits are pre-vaillingly rather dry at maturity those of the Agaricaceae are mostly fleshy although some dry forms occur. They are in the vast majority of the cases centrally stipitate, rarely laterally so, occasionally attached laterally without a stipe or even partially resupinate. In size the pileus may vary from a few millimeters in diameter in some species of *Marasmius* to 40 cm. in specimens of an exannulate form of *Agaricus arvensis* collected by the author. A specimen of this size must be capable of producing an enormous number of spores since Buller has shown that a not unusually large specimen of *Agaricus campestris* can produce 16,000,000,000 spores.

In general the basidia are club-shaped, varying to ovoid or to cylindrical. Usually four basidiospores are produced although frequently the basidium may become eight nucleate. The mycelium in the vicinity of the gills and in the gills themselves is normally of secondary (dicaryon) type and this is usually true of the whole spore-fruit, although sometimes the portions more remote from the hymenium are of the primary (monocaryon) type. In the tissues of the pileus the more slender hyphae usually show the clamp connections while often those of greater thickness fail to show them although directly connected to the others.

The species of Agaricaceae may be "homothallic" or "heterothallic" and bipolar or quadripolar. Most genera of the Agaricaceae have not been grown in culture so that it is not known how extensively the occurrence of two or more sexual phases is to be found. The phenomena of sexuality have been discussed rather fully in the preceding chapter.

The Agaricaceae are mainly saprophytic, living on the ground, decaying leaves, bark, wood, manure, etc. Some species of *Nyctalis* and *Volvaria* are parasitic on other Agaricaceae. *Armillaria mellea* (Figure 116) attacks the roots of trees and kills their cortical tissues, growing up in the living portion of the bark of the tree trunk and causing the death of the tree. It may continue to live as a sapro-

phyte in dead roots and old stumps. It is especially destructive to apple and cherry trees planted where previously there were oaks or other trees on whose roots this fungus once grew parasitically, continuing to live as a saprophyte until the apple or cherry roots became available. *Agaricus campestris* and one or two other species



FIG. 116.—Agaricales, Agaricaceae. *Armillaria mellea* on *Thuja occidentalis*. (Original, Dow V. Baxter.)

are cultivated for food and many wild species are collected for this purpose (Figure 117). Among these may be mentioned *Lepiota naucina* and *L. procera*, various species of *Agaricus*, *Pluteus cervinus*, *Pholiota adiposa*, *Ph. praecox*, *Coprinus comatus* (Figure 118), *C. atramentarius*, *Hypholoma appendiculatum*, *Cantharellus cibarius*, various species of *Hygrophorus*, *Marasmius caryophyllus* (*M. oreades*), *Lactarius volemus*, *L. deliciosus*, *Pleurotus ostreatus*, *Pl. ulmarius*, *Collybia radicata*, *C. velutipes*, *Clitocybe infundibuliformis*, *Tricholoma personatum*, *Tr. equestre*, *Armillaria mellea* (Figure 116), *Amanita rubescens*, *A. caesarea* and many other species of the



FIG. 117.—Agaricales, Agaricaceae. *Agaricus rodmani*. (Original, F. C. Strong.)

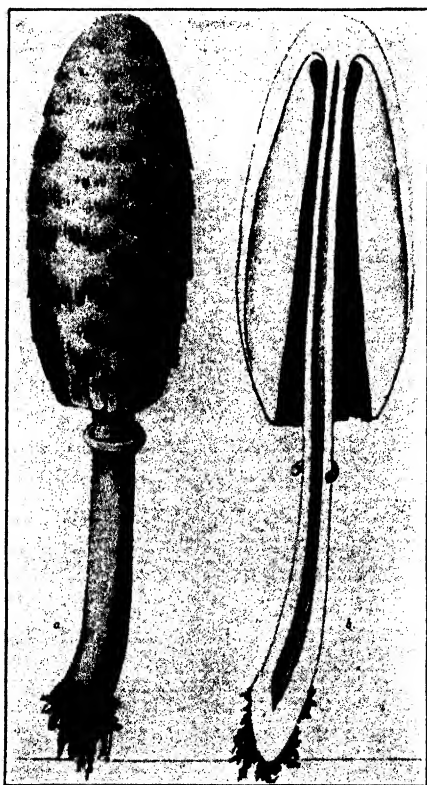


FIG. 118.—Agaricales, Agaricaceae. *Coprinus comatus*. (After Farlow, 1898.)

foregoing and other genera. On the other hand many species are poisonous, some mildly so, some dangerously. *Amanita phalloides* and its close relatives are so poisonous that a piece one cubic centimeter in size will cause severe illness if not death, there being no known antidote for this poison. *A. muscaria* (Figure 119) is also

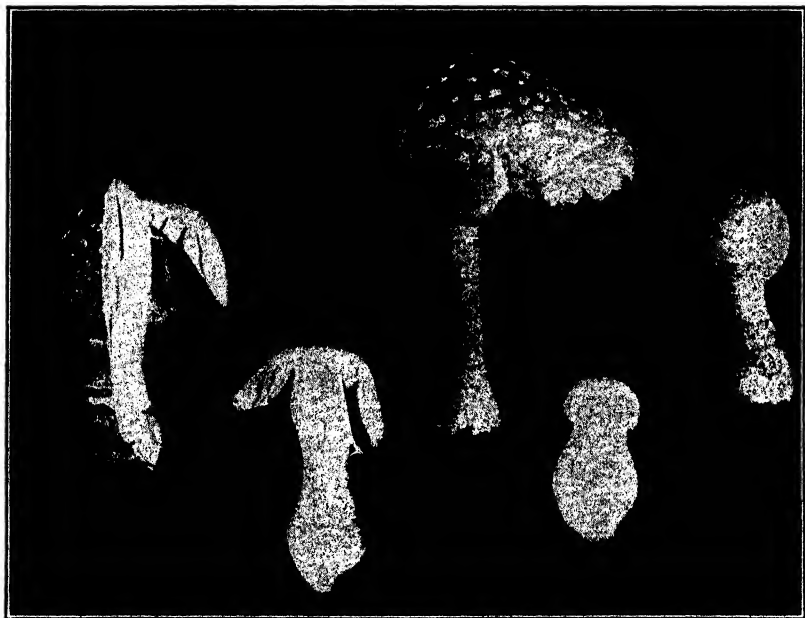


FIG. 119.—Agaricales, Agaricaceae. *Amanita muscaria*. (Original, F. C. Strong.)

dangerously poisonous although it is used as an intoxicant by some of the tribes native to Siberia. Unless one is very familiar with the species of *Amanita* it is well to avoid all, even the edible species of the genus. *Lepiota morgani*, a species with greenish spores, is poisonous to some persons, although other species of the genus are edible. Several species of *Tricholoma* are poisonous. *Clitocybe* (*Monadelphus*) *illudens*, whose orange colored spore fruits shine at night when fresh, is also poisonous as are various species of *Russula*, *Entoloma*, *Cortinarius*, *Hebeloma*, *Inocybe* and of other genera many of whose species are edible. The popular designation of the poisonous species as toadstools although etymologically correct (Todes

Stuhl, death's chair) is not botanically correct, for all members of the family, at least those with central stipes, are toadstools regardless of their edibility or toxicity. The word mushroom is also generally applied to all forms. It may well be noted here that no simple test such as the staining of a silver coin upon cooking with the fungus or the ability to peel the pileus is a safe criterion to use in judging the edibility of a species. Each species must be known with absolute certainty by its appearance, habitat, etc.

In general the tissues of the pileus are made up of slender, more or less closely packed hyphae on which usually clamp connections can be observed. Frequently there are numerous hyphae somewhat larger in diameter and constricted at the septa. In the genus *Russula* there are large bladder-like cells, perhaps for storage purposes, among the slender hyphae. In *Lactarius* there are large latex-containing cells and vessels in the pileus and extending into the trama of the gills and even into the stipe. The latex may be white, pink, yellow, green, blue or even colorless. It may remain unchanged or may change color on exposure to the air. Because of the presence of these large bladder-like cells these two genera have sometimes been set off by themselves as representatives of a distinct family, the Lactariaceae.

A study of the development of a typical spore-fruit of a centrally stipitate member of the family shows that the hymenial surfaces are enclosed and protected until the spore-fruit is almost mature and has begun to expand. The young spore-fruit is more or less spherical, the central axis being occupied by the short vertical stipe at whose top the pileus is attached. This curves downward, enclosing the stipe. A circular chamber appears surrounding a portion of the stipe and into this constantly enlarging chamber the gills protrude from the inner surface of the pileus until their edges come more or less completely in contact with the stipe. At the approach of maturity the stipe elongates and the pileus begins to expand, its edges pulling away from the stipe. Thus the edges of the gills become exposed to the air. As the pileus expands the gills become separated from each other more and more until there are distinct spaces between all of them. The stipe always grows in such a position, curving if necessary, that the pileus stands with the gills exactly vertical. In some species (e.g. of *Coprinus*) long cells (cystidia) grow from one gill surface across the interlamellar space

to the next gill, holding them apart the right distance (Figure 115, A). The basidia up to this time have been immature, but now they shoot off their spores with sufficient violence to carry them part way across the interlamellar space, when they fall downward until they reach the outer air below the gills and are carried away by the air currents.

Aside from the characters already mentioned there are many others used in distinguishing the 70 to 100 or more genera into which the 5000 to 6000 species are divided. The attachment of the pileus is of importance, i.e. laterally attached without stipe or laterally stipitate or centrally stipitate. Other questions to be answered before identification can be made are the following: Are the tissues of the stipe continuous with and similar to the tissues of the pileus or of different nature, and in the latter case do the pileus and stipe easily separate? Is the trama of the gills continuous with the tissue of the pileus or are the gills easily separable? Do the gills come into contact with the stipe, and if so are they adherent to it and decurrent or do they form a little notch where they meet the stipe? When young the spore-fruit sometimes has a layer of tissue, the universal veil, surrounding the whole structure. As the stipe elongates and the pileus expands this veil is stretched and may rupture at various points. It may leave a cup-like structure, the volva, around the foot of the stipe, adhering only loosely or grown fast to the stipe (Figure 119). On the pileus it may remain as patches or scales (Figure 119) of various size and conspicuousness or be apparent only as adnate silky fibrils. A second or inner veil may extend from the edge of the pileus to some point on the stipe, thus enclosing the developing gills in a closed chamber. Upon expansion of the pileus this veil may pull loose from its edge and remain as a loose or firmly attached collar, or annulus (Figure 118), on the stipe or it may tear loose from the stipe and adhere to the edge of the pileus as a cobwebby or membranous cortina. Both the universal and inner veil may be present or both may be absent or only one or the other.

The usual classification of the genera of the Agaricaceae is confessedly an artificial one being based primarily upon the color of the spores. The subdivisions are as follows: spores hyaline, *Leucosporae*; yellow to ochre-color, *Ochrosporae*; pink to red, *Rhodosporae*; purple-brown, *Amaurosporae*; black, *Melanosporae*. Sometimes the last two groups are united under the last name. The characters mentioned in the preceding paragraphs are used to sub-

divide each of these groups. Another feature considered is whether the pileus decays at maturity or dries out and revives when moistened again. The shape of the pileus is of importance as is the character of the stipe, whether cartilaginous or fleshy, hollow or solid, etc. In *Coprinus* the pileus and gills undergo autodigestion into an inky fluid from the edge progressively toward the stipe (Figure 115, A), this autodigestion affecting only those portions of the gills that have already shed their spores. The shape and size of pileus, gills, and



FIG. 120.—Agaricales, Agaricaceae. *Pleurotus sapidus*. (After Atkinson, 1900.)

stipe, their color, presence or absence of hairs or scales, the size and shape and markings of the spores are all characters that are used in specific distinctions, less often for generic distinctions. The presence or absence of cystidia and their shape and location when present, the branching or non-branching of the gills, etc. are also characters of which use is made. The result of using the spore color as the primary means of subdivision results in separating otherwise similar genera into different groups. Thus *Pleurotus* (Leucosporae), *Claudopus* (Rhodosporae) and *Crepidotus* (Ochrosporae) are laterally attached, more or less shell like, with gills decurrent and, except for the spore color, very similar (Figure 120). *Lepiota* (Leucosporae), *Annularia* (Rhodosporae), *Pholiota* (Ochrosporae) and *Agaricus* (*Psalliota*) in the Amaurosporae, have a fleshy pileus more or less easily separable from the central stipe which bears an annulus.

It seems probable that from an evolutionary standpoint the spore color is a later development and not of fundamental importance. It is worthy of notice that Pietro Antonio Micheli in 1729 published what is probably the first key to the species of this family which he recognized merely as the single genus *Fungus*. Among the characters used by him in his key were the clustered or separate growth of the spore-fruits, their branching or non-branching, presence or absence of volva, presence or absence of annulus, nature of annulus, i.e. whether free or attached to the stipe, presence or absence of striations on the pileus, location of striations if present, whether pileus and gills were of the same or of different colors, presence or absence of latex, etc. Although his system, too, was largely artificial it served to distinguish the species known to Micheli and in some particulars was no more artificial than the one now currently employed.

Among the Leucosporae the genus *Cantherellus* with its rather thick, low, more or less waxy decurrent gills on a frequently funnel-shaped pileus resembles very closely the genus *Craterellus* of the Thelephoraceae, which often has low folds like rudimentary gills. Doubtless the two are closely related. However, since *Craterellus* differs from most of the Thelephoraceae in being fleshy instead of leathery it is possible that it does not belong in that family at all but is merely a derivative of *Cantherellus* with less pronounced gills. If the latter is the case the direct derivation of the Agaricaceae from the Thelephoraceae, via *Craterellus* is impossible. In the Ochrosporae the genus *Paxillus* with its more or less anastomosing gills easily separable from the pileus reminds one of the genus *Boletinellus* of the Boletaceae. In the latter genus the "pores" are formed by radiating lamellae connected by cross partitions, and are also separable from the pileus. Its spores, too, are ochre colored. In fact *Boletinellus merulioides* was originally called a species of *Paxillus*. As in the case of the relationship of *Craterellus* and *Cantherellus*, *Boletinellus* may be but a derivative of *Paxillus* and not a connecting link between the Agaricaceae and Boletaceae. A somewhat similar condition exists with reference to *Lenzites* and *Daedalia* in the Polyporaceae and *Lentinus* (Leucosporae) in the Agaricaceae. Undoubtedly the Thelephoraceae, Boletaceae, Polyporaceae and Agaricaceae are closely related but just what path the course of evolution followed is not at all clear. Within the family it

seems likely that those genera with hymenium exposed all the time, as in *Cantherellus*, *Lentinus*, *Pleurotus*, etc. are more primitive than those in which the gills are formed in an internal cavity, becoming exposed only near maturity. Thus the forms with an annulus or cortina would represent an advance over those strictly gymnocarpous forms while those with a well developed universal veil and volva may be looked upon as the culmination in this direction of evolution.

In the Leucosporae the genus *Clitocybe* with its usually narrow, sharp-edged, decurrent gills and frequently funnel shaped pileus is clearly closely related to *Cantherellus*. *Armillaria* is quite similar to *Clitocybe* but differs in the possession of an annulus. In *Lepiota* there is an annulus as in *Armillaria* but the stipe is separable from the pileus. *Lepiota procera*, the edible "parasol mushroom" sometimes attains a height of 40 cm. and a pileus diameter of 15 cm. or more. Closely related to *Lepiota* is *Amanita* with both annulus and volva. The species of this genus are mostly inhabitants of forests and with few exceptions are dangerously poisonous.

In Ochrosporae aside from *Paxillus*, already mentioned above, the genus *Cortinarius* with over 300 species is of importance. The veil in this species instead of being membranous is cobwebby and remains attached to the edge of the expanded pileus for a short time. The fungi are of good size and vary in color, some being brown, yellow, violet, etc. Some species are strongly suspected of being poisonous. *Pholiota* with a distinct but sometimes evanescent annulus contains about 100 species. *Ph. adiposa* grows on tree trunks in clusters. It is yellow, with separable scales on the pileus, which is very viscid. The stipes are long and stout. It is found in the fall and is one of the latest of the wild edible species.

The Rhodosporae include the genus *Pluteus* with the stipe separable from the pileus and gills free from the stipe. Its species are mostly wood inhabiting. The edible *P. cervinus*, the deer mushroom, is common on piles of sawdust around old sawmills. *Volvaria* has a very large, loose volva which is often split into several lobes. Some species grow on wood, others are parasitic on other mushrooms. Some are edible but others are suspected of being poisonous.

Amaurosporae.—The genus *Hypholoma* has the stipe united with the pileus and of much the same character. The veil usually does not remain as an annulus but may leave fragments hanging down

from the edge of the pileus as a fragmentary cortina. The edible *H. appendiculatum* grows in clusters around stumps or on wood buried in the ground. Its fragile gray spore-fruits with pink to purple brown gills are very delicious when properly cooked. *H. sublateralitium* grows in clusters on tree trunks. Its pileus is brick red, in the center at least. It also is edible. *Stropharia* resembles *Hypholoma* but has a distinct annulus. *Agaricus* (= *Psalliota* of many authors) has a stipe easily separable from the pileus. It has a well developed annulus. The gills are at first white then pink and ultimately purple brown or almost black. The fungus is usually found on the ground in the woods or in meadows. *A. campestris* is common in the late summer in pastures and meadows as is the usually larger *A. arvensis*. The latter has a double annulus and the gills are slow in turning pink and remain pink only a very short time. Both are edible. The former is the common cultivated mushroom.

Melanosporae.—The commonest genus is *Coprinus* whose pileus and gills deliquesce into a black ink. The edible *C. comatus*, the shaggy-mane mushroom, is perhaps the largest species of the genus. The largest specimen seen by the author was one described by Blodgett, 36 cm. tall, 25 cm. in circumference of the pileus and 9 cm. in circumference of the stipe. The pileus weighed 500 grams. *C. micaceus* is very common in crowded clusters at the bases of deciduous trees. It produces its spore-fruits periodically during the season, at intervals of 1 to 4 weeks depending upon the frequency and amount of rain. There may be six to eight crops during the season, from Spring till early Fall.

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CHAPTER XIII

BASIDIOMYCETAE: GASTEROMYCETAEAE

The name Gasteromycetaceae (often spelled Gastromycetaceae) is given to a group including those orders of Basidiomycetaceae which have single-celled, mostly 4-spored basidia produced within closed spore-fruits. These may have definite means of dehiscence by means of which the spores reach the exterior or they may depend upon animals which feed upon the spore-fruits and thus carry the spores to various places, or the spores escape only upon the decay of the spore-fruits. Mostly the basidia are produced in a hymenium which lines a closed cavity, but the latter instead of being exposed to the air at time of spore formation, as in the Agaricales, remains closed until after the spores have been produced. Frequently the spore-fruits are produced underground, emerging as they approach maturity or remaining subterranean. Other forms grow on stumps, logs, etc. The mycelium usually shows the presence of clamp connections. Conidia are known in a few forms. Sexual reproduction is practically unknown. Few species of this group have been grown successfully in culture. Even the germination of the spores has been found to be impossible in many species. The basidia may be clavate or cylindrical as in the majority of the Agaricales but in the main are more inclined to be ovoid or globose with sterigmata varying from short to long. Sometimes the long sterigma remains attached to the spore, like the handle of a drumstick. The spores are not shot from the sterigmata with violence as in the preceding order. The young basidia are binucleate and the two nuclei unite, this union being followed by meiotic divisions leading to the production of four haploid nuclei. The first meiotic spindle is transverse in the majority of cases but is sometimes longitudinal. In some cases subsequent divisions produce eight nuclei or even more. Usually the number of basidiospores is four, but not rarely 6 to 8 and in rare cases up to 12 spores are produced. These are always at first uninucleate but in most of the few cases studied they early

become binucleate by the division of the original nucleus. Whether this is the origin of the dicaryon phase of mycelium is unknown. Lorenz has shown for *Sphaerobolus grandis* that basidiospores give rise to monocaryon mycelium. These mycelia show two sexual phases, i.e. this species is sexually bipolar, and only when the appropriate mycelia are mated does a dicaryon mycelium with clamp connections arise. In this species the basidiospores are uninucleate, although some species of this genus have been described as producing binucleate spores.

In general the structure of the spore-fruit in the Gasteromyceteae is as follows: Externally there is a peridium consisting of one or more layers. It may be firm and hard (*Scleroderma*) or soft and papery or may even disappear during the development of the spore-fruit, being present only in the very young stages (*Gautieria graveolens*). Within the peridium the tissue may consist simply of the gleba (Figure 126) or of the gleba traversed by "veins" or by a "columella" or by both (Figures 121, 122, 131). The gleba consists of a more or less fleshy mycelial growth containing numerous hymenium-lined cavities (hymenial cavities). The columella and veins are slender or stout strands of hyphae having several functions; food conduction, support and in some cases the dehiscence of the spore-fruit at maturity. The gleba in many genera undergoes autodigestion after the basidiospores have been formed. The tissues involved are the basidia and the fungus tissue lying between the hymenial cavities. As a result nothing is left of the gleba except the basidiospores or also a few stiff threads, the capillitium. These are simple or branching thick-walled hyphae, which develop in the inter-hymenial tissues of the gleba before maturity. They are rarely septate. The tangled mass of capillitial hyphae prevents the escape of all the spores at once, permitting them to sift out a few at a time. In some cases hymenial cavities with a definite layer of hymenium are wanting but clusters of basidia appear here and there in the gleba (Figure 129, A).

Because of the lack of study of the younger stages of development of the spore-fruits in many of the genera it is impossible as yet to arrange the known species in a satisfactory system with any confidence that it indicates the true relationships. Indeed, the various views held reflect this uncertainty. Whereas thirty years ago the Gasteromyceteae were confidently divided into the five orders,

Hymenogastrales, Sclerodermatales, Lycoperdales, Phallales and Nidulariales, the developmental studies made more recently have shown that the sharp distinctions between the first and second named orders do not hold completely while on the other hand the first order falls into two very distinct divisions. Just where ordinal lines should be drawn and which types are the more primitive is very uncertain and even the direction of evolution in some of the groups is a matter of great doubt.

The question as to the origin of the Gasteromyceteae remains to be solved. It has been suggested by Gäumann and by Mez that some of the simpler Thelephoraceae may have undergone folding of the surface destined to bear the hymenium in somewhat the manner of *Hemigaster*. In this genus an upright column of mycelium spreads at the apex and recurves to the main stalk, thus forming an annular cavity whose upper and outer sides produce a hymenium. On the other hand the plane hymenial surface of some forms similar to *Corticium* may have become more and more wrinkled and folded, with the outer exposed surfaces losing their hymenium and the infolded and finally completely closed cavities retaining it. Another suggested origin is from the Agaricaceae. Such genera of the latter as *Agaricus* or *Amanita* are essentially angiocarpous until just before the basidiospores are formed. If the spores should be formed in *Amanita* before the fruiting body opened up and the gleba (in this case represented by the gills) should disintegrate we should have a condition much like that in some of the Hymenogastrales (*Secotium*) or Phallales. A third possible origin would be from the subterranean Ascomyceteae such as the Tuberales, by the conversion of the asci into basidia. Against this hypothesis is the doubt whether so highly specialized a group as the Tuberales could give rise to a new phylogenetic line of such great fertility of evolution of forms.

In the classification followed below the Hymenogastrales are first considered, as from this order (in its wider sense) appear to have arisen the other orders of this great group.

Order Hymenogastrales.—Almost exclusively soil inhabiting fungi, with their spore-fruits subterranean or emerging at maturity. These vary from a few millimeters to several centimeters in diameter and are spherical to ovoid, sometimes considerably elongated in the vertical direction. The peridium is delicate to firm and thick, disappearing before maturity is reached in some species of *Gautieria*

(Figure 121). It may be indehiscent or irregularly or regularly dehiscent. The gleba may fill the whole interior or may be traversed by a columella or by radiating or otherwise arranged sterile veins, or by both. It may contain definite cavities lined by hymenium or these may be replaced by knots of mycelium containing irregularly arranged basidia. In one or two genera the tramal tissues, i.e. those lying between the hymenial cavities, split so that these are set free

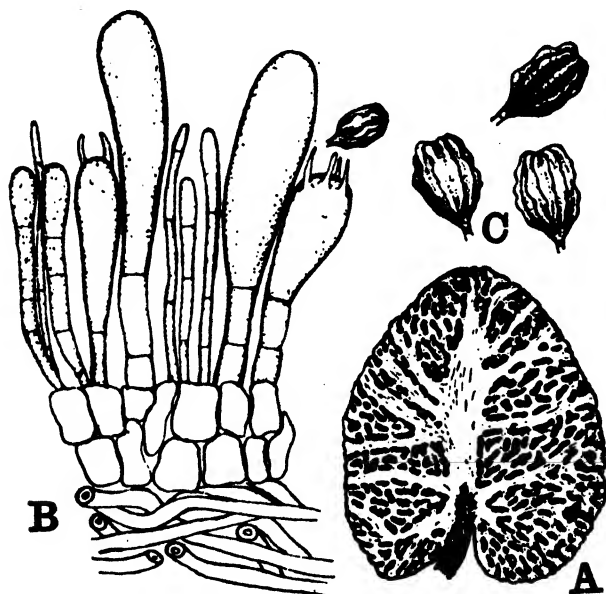


FIG. 121.—Hymenogastrales. *Gautieria plumbea*. A, vertical section of fruiting body; B, portion of hymenium; C, basidiospores. (After Zeller and Dodge, 1918.)

as small hollow bodies, the peridioles. In other genera the tramal tissues disintegrate, leaving the basidiospores and a few threads of capillitium. In still others the elongation of the columella ruptures the peridium and the gleba is exposed to the air where it weathers away or decays, thus setting free the spores. In some of the indehiscent genera the spores are set free by the decay of the spore-fruit or by rodents which feed upon it. The basidia are ovoid to clavate, mostly four spored but in some cases with six or more spores. The spores are at first uninucleate but seem in most cases to become binucleate very soon. Zeller and Dodge have shown that conidia

also are produced within the spore-fruit in a few forms that they have carefully studied. In *Archangeliella* these authors found cells of oidial character produced externally. The mycelium is dicaryon in nature, with clamp connections.

The spore-fruits usually arise as enlargements at the ends of strands of mycelium. In some cases the various stages of development have been followed but in the majority of forms only the mature structures are known. The interior of the young spore-fruit is at first a dense, uniform mass of hyphae. In some genera these hyphae become more densely compacted in places and correspondingly loosely arranged in between. These looser tracts eventually become more or less sinuate cavities lined by basidia which arise from the firmer tissues as a palisade. The cavities become larger as the tramal tissues become compressed. In some other genera a central axis, or columella, traverses the spore-fruit from the base towards or to the peridium at the apex. From it may grow out irregular "tramal plates" which branch and anastomose. On their surface arise the hymenia. In other forms the tramal plates grow inward from the peridium or downward from the upper portion of the peridium (Figure 122, C, D). From mature spore-fruits it is not always clear whether the tramal plates have arisen from the transformation of a ground tissue filling the whole spore-fruit, as first described, or by growing out from the columella or peridium. Eduard Fischer in Switzerland and C. W. Dodge in this country have contributed most to our knowledge of this group. The following families may be given consideration:

FAMILY RHIZOPOGONACEAE.—The gleba occupies practically the whole of the interior of the spore-fruit. The differentiation of the hymenial cavities begins near the center and extends in all directions toward the peridium. The latter is usually rather delicate and may slough off in some forms. Usually the hymenial cavities are well marked but in a few transitional forms they are loosely filled by mycelium with scattered basidia, as in the next family. No capillitium is formed and the spores escape by the decay of the spore-fruit or its consumption by insects or rodents. The basidiospores are ellipsoidal or almost spherical, and smooth. *Rhizopogon* forms subterranean spore-fruits 2 to 5 cm in diameter and with root-like mycelial strands attached at various points. The peridium is membranous or leathery and not easily separable from the gleba

which contains irregular or labyrinthiform hymenial cavities. The basidiospores are mostly 6 to 8 to each basidium. *Melanogaster* is quite similar except that the basidia are irregularly scattered throughout the hymenial cavities instead of forming a hymenial lining. *Leucogaster* has the hymenial cavities filled with a mass of jelly, the remains of conidium-like structures formed before the hymenium develops.

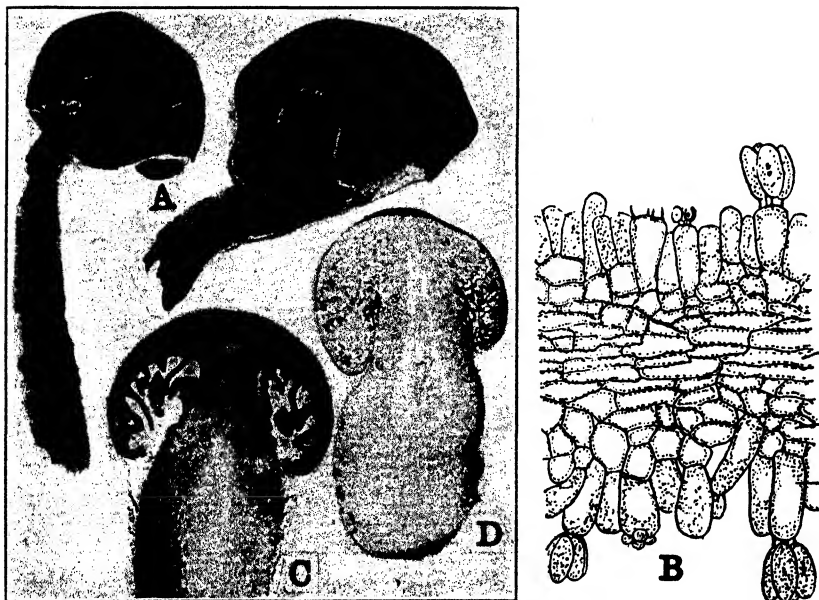


FIG. 122.—Hymenogastrales. *Secotium erythrocephalum*. A, mature plant; B, section of tramal plate; C, vertical section through young plant; D, vertical section through nearly mature plant. (After Cunningham, 1925.)

FAMILY SCLERODERMATACEAE.—In this family the hymenial cavities are largely filled with mycelium bearing scattered tufts of basidia. This was formerly the basis for setting this family apart from the others as a separate Order Sclerodermatales (or Plectobasidiales), but the occurrence of similar structures in other families or even genera in which typical hymenial cavities occur makes this character of minor importance. The gleba produces some capillitial threads. The peridium is thick and ruptures irregularly or by lobes, exposing the brown mass of spores and capillitium. In *Scleroderma* the thick peridium is separable from the gleba, and opens at the top

by an irregular opening or in some cases by splitting into definite lobes. In *Pisolithus* the trama tissue dehisces between the knots of basidia so that the rupture of the peridium permits the escape of little masses of tissue containing internally the irregularly tangled hyphae bearing the basidia and the basidiospores.

FAMILY HYMENOGASTRACEAE.—The spore-fruits of this family resemble very much those of the Rhizopogonaceae (which are sometimes united with it) but the development of the hymenial chambers begins at the top of the spore-fruit, progressing downward to the base or to a sterile basal portion which may be low or may reach upward in the central axis nearly to the apex as a "columella." The peridium is rather thin and may disappear before the spore-fruit attains its full size. *Hymenogaster* resembles *Rhizopogon* in many particulars but lacks the root-like mycelial strands. The spores are lemon shaped. *Hydnangium* with similar development has spherical, echinulate spores and is sometimes placed in a distinct family, the Hydnangiaceae.

FAMILY HYSTERANGIACEAE.—In this family a simple or branched columella reaches nearly or quite to the top of the spore-fruit where it joins with the peridium. From this columella and sometimes from the apical portion of the peridium occurs the development of the gleba by the growing out of tramal plates which branch and unite to form the hymenial cavities (Figure 122). In some forms the peridium grows outward and downward from the top of the stipe-like columella and curves inward to join the stipe again. By the outgrowth of tramal plates from the columella and downward from the peridium the space between columella and peridium becomes filled with the gleba before the spore-fruit is entirely closed. In *Secotium* (*Endoptychum*) *agaricoides* the tramal plates are radial in arrangement. When the stipe elongates at maturity a portion of the gleba and the lower edge of the peridium are pulled free from the stipe. The presence of cystidia in the hymenium of some species of *Secotium* lends greater similarity to the Agaricaceae to which some authors unite this genus. *Podaxis* is very similar to *Secotium*. *Phallo-gaster* has a branching columella, the apices of the branches spreading out in disk-like plates in contact with the peridium. The gleba is formed by the outgrowth of tramal plates from the branches of the columella, filling the space between the latter. At maturity the gleba is transformed into a greenish slimy gel and the

peridium dehisces at various points between the plates at the apices of the columellar branches.

Order Nidulariales.—Bird's-nest Fungi.—In this order we find carried to an extreme the tendency shown by *Pisolithus* in the Sclerodermataceae. Instead of numerous masses of basidia and spores surrounded by small amounts of tramal tissue we find in this order a few peridioles, one to six or eight up to twenty. Each



FIG. 123.—Nidulariales. *Cyathus striatus* (*C. schweinitzii*). (Original, F. C. Strong.)

consists of a definite hymenial cavity lined with basidia and surrounded by several layers of firm tramal mycelium (Figure 124, A).

FAMILY NIDULARIACEAE.—Bird's Nest Fungi. Several peridioles are formed in each spore-fruit. At first connected in a continuous gleba the peridioles early become separate from each other and lie free in the cavity of the spore-fruit or are connected to the peridium by long slender strands, the "funiculi." The principal genera are *Crucibulum*, *Cyathus* (Figure 123, 124) and *Nidularia*. The spore-fruits are several millimeters up to a centimeter in height and funnel-form or almost spherical with a flattened top. The peridium on this flattened upper portion ruptures and exposes the peridioles

lying like eggs in a nest (Figure 123), whence the common name of the fungi. Rain and wind distribute the peridioles to various distances. They have no means of dehiscence and the spores can escape only by decay of the peridiolar walls, or germinate within the peridiole.

FAMILY SPHAEROBOLACEAE.—The single genus, *Sphaerobolus*, produces but one peridiole. By special adaptation the thick inner

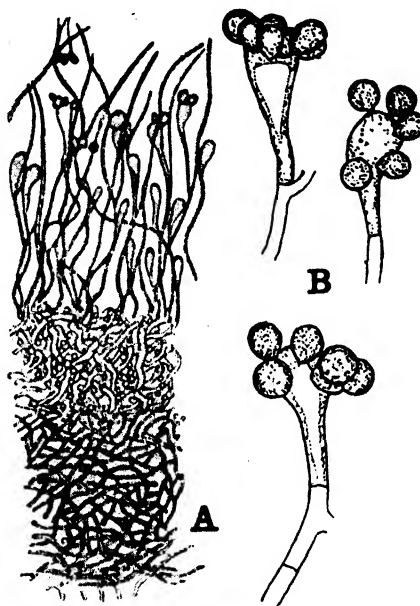


FIG. 124.—Nidulariales. *Cyathus stercoreus*. A, section of wall of young peridiole; B and C, basidia. (After Coker, 1928.)

layer of the several layered peridium wall is everted with such violence as to throw the spherical peridiole, which is 1 to 2 mm. in diameter, to a height of 4 meters or even more. The basidia may have 8 to 9 spores in *S. stellatus*. In this species the basidia are irregularly arranged in clusters in the interior of the peridiole while L. B. Walker has shown that in *S. iowensis* the peridiole contains numerous typical hymenial cavities. The inclusion of the Sphaerobolaceae in the Order Nidulariales, although not unusual is probably not well grounded. The structure of the peridioles of the Nidulariaceae is quite different from the spherical glebal mass of *Sphaero-*

bolus. In the second edition of Engler and Prantl the latter is placed close to the Sclerodermataceae and Tylostomataceae.

Order Lycoperdales.—Puff-balls.—The order contains two families: Lycoperdaceae, with round to ovoid or pyriform epigaeous or epixylous spore-fruits without true stipe, and Tylostomataceae, with subterranean spore-fruits which are pushed from the soil at maturity by the elongation of a definite stipe. Sometimes this family is placed in a distinct order.

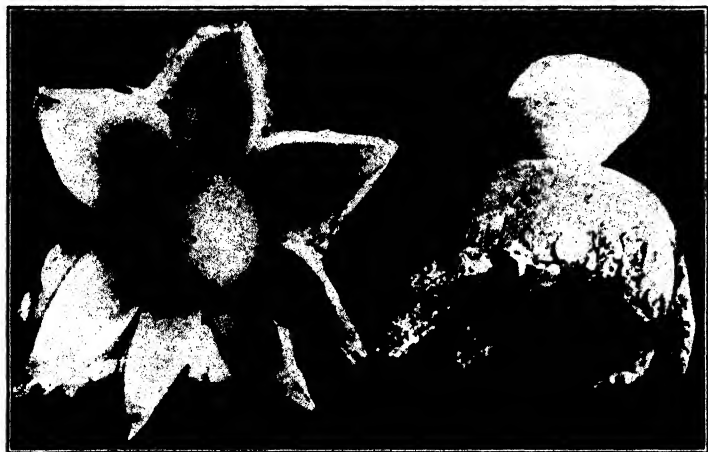


FIG. 125.—Lycoperdales. *Geaster rufescens*. (After Coker, 1924.)

FAMILY LYCOPERDACEAE.—The spore-fruits are external from the first or may be shallowly subterranean when young, becoming external at maturity. They consist of a flexible peridium of two to three well marked layers enclosing the gleba, which like that of *Rhizopogon*, develops its hymenial cavities from the center outwards. The basidia are ovoid with short or long sterigmata and 4 to 8 basidiospores. After the spores are mature the basidia and the tramal tissue dissolve, except for the brown, thick-walled capillitial threads. As the spore-fruit enlarges the outer peridium ruptures in various ways, scaling off in granules or larger pieces or folding back in lobes (*Geaster*, Figure 125). The inner peridium may also break up in pieces (*Calvatia*, Figure 126) or more often forms one or more ostioles in the apical region. As wind or firmer objects strike the spore-fruit the spores are puffed out through these ostioles. The

spore-fruits vary from a few millimeters in diameter up to 1.6 meters in length, 1.35 meters in width and 24 cm. in height, in the case of a specimen of *Calvatia maxima* collected in New York State some years ago and reported by C. E. Bessey. Such a puffball would produce approximately 160,000,000,000,000 spores. As in some of the Hymenogastreales the basal portion of the spore-fruit may remain sterile, not forming basidia in the cavities which are formed in this sterile base. This is particularly characteristic of the genus *Lycoperdon* in which the sterile base may be narrower and resemble somewhat

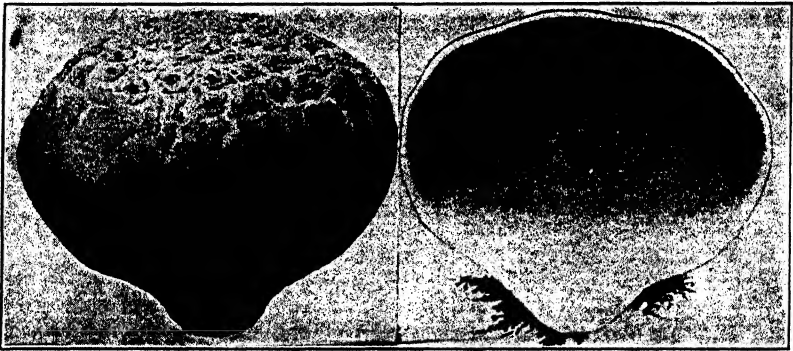


FIG. 126.—Lycoperdales. *Calvatia cyathiformis*. (After Farlow, U.S.D.A., 1898.)

a broad stipe. In *Calvatia* the basal portion is sterile in some species but not markedly narrowed. The spore-fruits of all the species of this family appear to be edible when young, while still white and rather brittle. The genus *Lycoperdon* has many species varying in size from 1 cm. to 5 cm. or more. The spore-fruits are more or less pear-shaped with large sterile basal portion. The exoperidium scales off as granules or scales. The endoperidium has a single apical ostiole. They grow scattered or in closely crowded masses on the ground (Figure 127) or on decaying wood. *Calvatia* differs externally from *Lycoperdon* in the less pronounced narrowing of the sterile base and in the absence of an ostiole in the endoperidium. The latter breaks off in large pieces. *Calvatia maxima* occurring in the Fall in fields and pastures is collected while still firm and white for food. *Bovista* has a thin exoperidium which sloughs off and a slightly thicker endoperidium with an apical ostiole. There is no sterile base, the gleba filling the whole spore-fruit. The branched capillitial hyphae are slender and smooth. The sterigmata break

loose from the basidium and remain attached to the basidiospores. *B. plumbea* is 3 to 5 cm. in diameter, nearly round and with a lead-gray endoperidium. *Mycenastrum* has a rather thick endoperidium which cracks open in a more or less stellate manner. The capillitium is composed of thick, branched, spiny hyphae, tapering from the middle to the acute tips. The sterigmata are very short so that the spores are almost sessile. *Catastoma* (*Disciseda*) has a firm

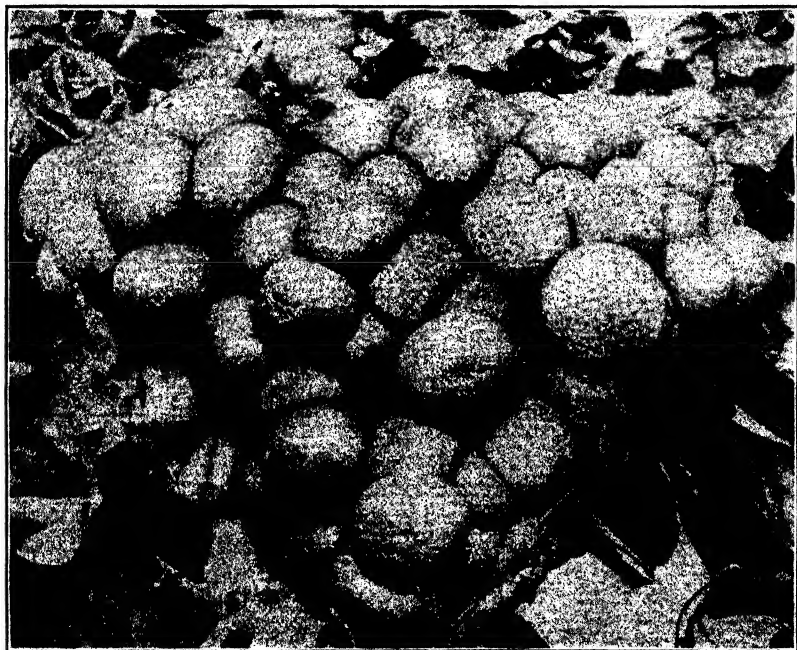


FIG. 127.—Lycoperdales. *Lycoperdon gemmatum*. (Original.)

exoperidium which splits equatorially. The endoperidium pulls free from the basal half of the exoperidium while remaining firmly attached to the upper half. The result is that the spore-fruit escapes and blows around, leaving the basal portion of the exoperidium still attached to the ground. The ostiole pierces the endoperidium at the center of the exposed portion, which is morphologically its base. *C. circumscissum* is common in grassy places in the prairie regions of the United States and in similar regions in Eastern Europe. In *Geaster* the outer peridium splits longitudinally

and curves out in pointed lobes, forming a stellate structure upon whose center lies the sessile or short stalked body of the spore-fruit encased in its thin endoperidium. The common name "Earth Star" is very appropriate (Figure 125). The endoperidium has one or several ostioles. A more or less evident columella may extend from the base part way toward the apex. *Broomeia* is a tropical genus with a stout stromatic base bearing on its upper surface a large number of small spore-fruits about 1 cm. in diameter, packed closely side by side, each opening by an apical ostiole.

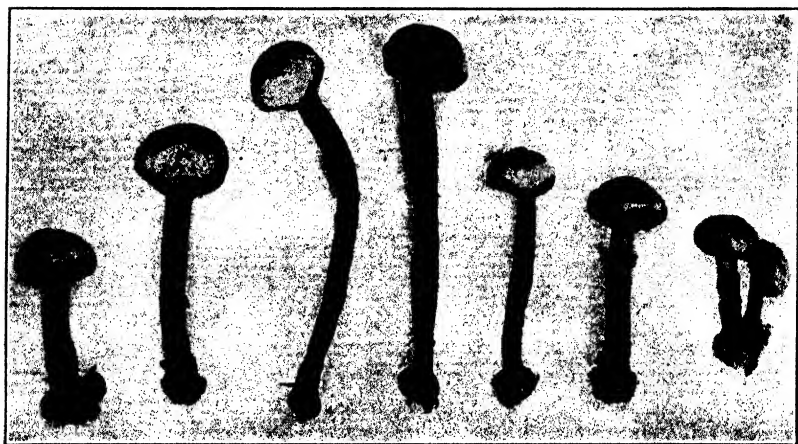


FIG. 128.—Lycoperdales. *Tylostoma campestre*. (Original.)

FAMILY TYLOSTOMATACEAE.—Stalked Puffballs.—The spore-fruits of this family originate hypogaeously but by the elongation of a basal stalk become epigaeous. The commonest genus is *Tylostoma* with a spherical spore-fruit 1 to 3 or 4 cm. in diameter and a slender stalk sometimes 5 or more centimeters in length and 2 to 4 mm. thick (Figure 128). The endoperidium opens by an apical ostiole which may be irregular or which may have a projecting striate margin. The 40 or more species are mostly found in drier regions. In some species the basidia are described as producing four basidiospores laterally instead of apically (Figure 129, *B*). Whether this is true for the whole genus or for other genera of the family is not known. The hymenial cavities in this genus and possibly other genera become obliterated by the growth into them of the hyphae bearing the irregularly arranged basidia as in *Scleroderma* and

Sphaerobolus stellatus (not as in *S. iowensis*) and in *Geaster* (*Astraeus*) *hygrometricus* (not in some other species of *Geaster*). For this reason the family is sometimes removed from the Order Lycoperdales. *Battarea* has a stout stalk that may reach 20 cm. in height. The endoperidium splits circumscissilely, rolling upwards a little at a time as the spores and capillitium escape. The gleba in this genus contains typical hymenial cavities. It is found in the sandy or gravelly soil of the foot-hill regions of the Rocky Mountains as well as in Europe. Another genus probably belonging in this family is

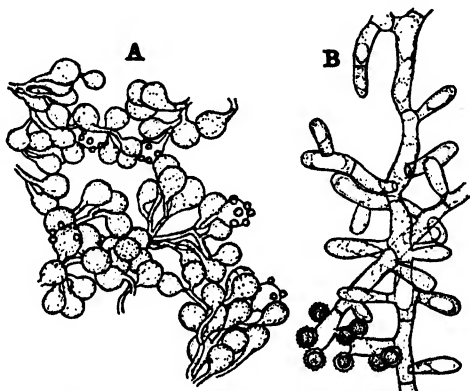


FIG. 129.—Lycoperdales. A, portion of gleba of *Geaster* (*Astraeus*) *hygrometricus*, showing partial obliteration of hymenial cavities; B, portion of gleba of *Tylostoma simulans*. (After Coker, 1928.)

Queletia. It has a stout stalk and the endoperidium breaks away in pieces to expose the capillitium and spores.

Order Phallales.—In this order the Gasteromyceteae attain their highest development. The spore-fruits are at first hypogaeous or practically so, and more or less spherical. They are surrounded by a tough leathery peridium within which is a layer of tissues which dissolve into slime. Below that there is a frame-work which by its expansion ruptures the peridium and exposes the gleba to the air. The gleba itself digests into a greenish or brownish, mostly very evil-smelling slime, whose odor attracts carrion-loving insects which probably assist in the spore distribution. The understanding of the structure and development as well as of the probable relationships within the order we owe chiefly to the painstaking work of Eduard Fischer extending over a period of more than a decade. Two or three families are recognized:

FAMILY CLATHRACEAE.—In this family the expanding frame-work lies rather close to the peridium and between its branches or meshes the gleba is formed. The framework may be sessile or stalked. *Clathrus cancellatus* (Figure 130) forms a rounded, hollow, lattice-work, usually red in color, seated in the volva-like remains of the peridium. *Simblum sphaerocephalum* resembles slightly a *Clathrus*



FIG. 130.—Phallales, Clathraceae. *Clathrus cancellatus*. (After Lloyd, 1909.)

with a short stalk whose base is surrounded by the volva. *Anthurus borealis*, occasionally found in the United States, does not form a lattice work but has several fingers which spread apart at maturity at the apex of a volvate stalk.

Cunningham separates from the foregoing in a distinct family the genus *Claustula*, whose sessile spore-fruit is indehiscent. The framework forms a hollow sphere lined internally by the gleba.

FAMILY PHALLACEAE.—In this family the expanding stalk is topped by a loosely or closely adhering pileus whose smooth or pitted outer surface is covered by the gleba. In *Phallus*, the commonest representative of the family, the bell-shaped pileus is attached at the upper end of the hollow spongy stalk, hanging around its upper portion, but free from it. The outer surface of the pileus is pitted, these pits being filled when the stalk expands, by the greenish brown slime into which the gleba has dissolved. In *Dictyophora duplicata* between the bell-like pileus and the stipe is formed a layer of tissue, the indusium, which expands into a beautiful net-like skirt standing out around the stipe (Figure 131). It undoubtedly serves to make the spore-fruit more conspicuous to insects flying in the vicinity. *Mutinus caninus* has its red pileus adhering closely to the upper portion of the white or pink stipe. The surface of the pileus is nearly smooth. The odor is particularly disgusting.

It seems probable that the Phallales have arisen from the Hymenogastrales, perhaps through forms like *Phallogaster*. Certain of the

tissues (corresponding to the columella or veins of the Hymenogastrales) have been specialized as expanding organs which rupture the peridium and carry the dissolved gleba out into the air. The



FIG. 131.—Phallales, Phallaceae. *Dictyophora duplicata*, "egg," sectioned, and expanded fruit body. (After Coker, 1928.)

occurrence of transitional forms between the *Clathrus* and *Phallus* type of structure seem to warrant the retention of the two families in the same order although some authors erect two orders Clathrales and Phallales, respectively.

The classification followed above is in the main that of Gäumann and Dodge, in 1928. The arrangement used by Eduard Fischer is quite different. He divides the Gasteromyceteae into six Unterreihen, corresponding to the orders of this book: Hymenogastrineae, Sclerodermatineae (including Tylostomataceae and Sphaerobolaceae), Nidulariineae, Lycoperdineae (two families Lycoperdaceae and Geastraceae), Phallineae and Podaxineae. The first two and the last are included in the Hymenogastrales of this work.

A brief survey of the Basidiomyceteae reveals the following facts. The primitive forms were probably those with spore-fruits flattened on the surface of the substratum with at first considerable variability in basidium structure. The forms with one-celled basidia appear to have developed in two directions; to form on the one hand an exposed hymenium borne on various modifications of the spore-fruit, the Hymenomycetous line (Order Agaricales) and on the other hand by the infolding of the hymenium so that it became internal, a group, the Gasteromyceteae, in which the hymenium does not become exposed to the air until after the basidiospores have been formed. So little is known of the sexual process in the class that this knowledge can not be used in developing a system of classification. Whether the number of nuclei (four or eight) produced in the basidium and their arrangement are of significance must await much more extensive studies of the nuclear behavior in all groups of the class. At best the present systems of classification are only tentative.

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CHAPTER XIV

FUNGI IMPERFECTI: THE IMPERFECT FUNGI

There are a great many species of fungi of which the perfect stage is not known and which therefore can not find a place in the classes already discussed. By the term "perfect stage," as here used, is meant that stage in which the ultimate sexual structures are formed, e.g. zygospores, oospores, asci, basidia, teliospores. Most of the Phycomyceteae are so characteristic in their mycelial structures as well as in their modes of asexual reproduction that ordinarily the genus and even the species can be determined from the asexual stage alone. Thus the Imperfect Fungi are practically confined to those Higher Fungi in which the stage is lacking in which the asci, basidia or teliospores are produced. Since most of the Uredinales have very characteristic asexual stages the imperfect forms in this order are readily assigned to that group and are placed in one of the imperfect genera there, e.g. *Aecidium*, *Uredo*, *Caeoma*, etc. Thus it comes about that the Fungi Imperfecti, as ordinarily considered, include those fungi, not otherwise referable to their natural relationship (e.g. Phycomyceteae or Uredinales) whose true relationship can not be determined in the absence of the perfect stage. Judging by the rather exceptional presence of clamp connections, as well as by the similarity of the conidial stages to those in the Class Ascomyceteae it is probable that the great majority of species of Imperfect Fungi are really Ascomyceteae of which the perfect stage has not yet been connected with the imperfect stage or which have, perhaps, entirely lost the perfect stage. A few are doubtless Basidiomyceteae and Ustilaginales. In the first edition of Engler and Prantl, *Die Natürlichen Pflanzenfamilien*, Lindau recognized about 600 genera and 15,000 to 20,000 species. In a recent, as yet unpublished work on this group Dr. Harold B. Bender recognizes as valid 1331 genera.

The distribution of these many species into genera, families and orders is necessarily based only upon the asexual structures present.

Inasmuch as it has been demonstrated that fungi whose perfect stages show them to be of very different families may possess rather similar types of asexual reproduction it follows that genera based on the asexual reproductive forms are not necessarily assemblages of related species. As an example attention may be drawn to the genus *Gloeosporium*. In this genus the one celled, hyaline, ellipsoidal, straight or slightly curved conidia are produced, usually imbedded in a gummy substance, from short conidiophores packed in a palisade underneath the host epidermis which is ruptured by the mass of conidia. This type of asexual reproduction is found in some species of *Gnomonia* and *Glomerella*, both being genera in the Family Gnomoniaceae of the Order Sphaeriales. The fungus *Pseudopeziza ribis*, Family Mollisiaceae, Order Pezizales, also has a *Gloeosporium* type of asexual reproduction. A number of similar cases are known. Since the genera based upon asexual structures do not necessarily indicate true relationships of the included species the term "form genus" was suggested for such groups by Schroeter. It is in this sense then that the term genus is used for this class. On the other hand, as has been pointed out by several authors, including Petrak and Sydow, there is frequently a similarity in asexual structures among fungi considered to be closely related as judged by their perfect stage. Careful study has revealed in many cases that the form genera of the Imperfect Fungi can be subdivided into groups of species correlated with the perfect stages. Thus has come about on the part of some mycologists the breaking up of the larger genera into smaller more compact genera, on characters that would otherwise be considered of rather minor importance except for their correlation with groups of perfect fungi.

As the life histories of various fungi are studied by pure culture methods or by means of carefully controlled inoculations, from time to time an imperfect fungus is connected up with its perfect stage. This may perhaps be a species already known or may have been unknown theretofore. Klebahn, the German mycologist, has made many such connections. Strictly speaking, such a fungus, once its perfect stage is known, should be removed from the Fungi Imperfecti, but since the perfect stage is very often rare, or only to be found in some other season of the year than that in which the imperfect stage occurs it is customary to leave such species in the group to which they were assigned before the perfect stage was known, at least so

that they may be identified in the absence of the other stage. It often happens that the same species has several types of asexual reproduction so that it may appear in several different form genera.

The many species and genera are usually divided into four form orders as follows:

Order Sphaeropsidales.—Conidia produced within pycnidia or modifications of such structures. A pycnidium (Figure 132) is a perithecium-like structure and may be complete, like the perithecium of the Sphaeriales and Hypocreales, or only the top half may be present as in the perithecium-like spore-fruit of the Hemisphaeriales, or it may open by a longitudinal slit as in the apothecia of the Hysteriales or may be closed at first and finally open into a cup or saucer shaped structure, much like a miniature apothecium.

Order Melanconiales.—Conidia produced singly or in chains, often surrounded by a gummy mass, from conidiophores packed closely in a usually subepidermal or subcortical layer, the acervulus (Figure 133).

Order Moniliales.—Conidia formed on conidiophores which are separate, at least at their apical portions, or the vegetative mycelium breaking up into conidia (Figures 134–139). The conidiophores may be simple or branched, short or long, similar to the vegetative mycelium, or very distinct from it, but are never enclosed within a pycnidium nor packed laterally into a subepidermal or subcortical acervulus. They are always external at time of conidium production.

Order Mycelia Sterilia.—Imperfect fungi which lack all conidial formation, and which form sclerotia, rhizomorphs and various other forms of mycelium without spores.

Order Sphaeropsidales.—The 568* genera (with over 2300 species in North America alone) ascribed to this order are divided into four form families.

FAMILY SPHAEROPSIDACEAE (*Sphaerioidaceae* of some authors):

Pycnidia like typical perithecia or forming pycnidial cavities in a stroma; tough leathery to brittle, and dark colored. The spores often exude from the ostiole in damp weather in a worm-like mass, or cirrus, consisting of gum and embedded spores. This family contains 359 genera so that it has become necessary to devise some

* The figures for this order are taken from H. B. Bender's pamphlet on the Sphaeropsidales.

means of subdividing it in a practical and easily applied manner. The scheme most often used was suggested by the great Italian mycologist P. A. Saccardo and is based on the structure and color of the spores, as follows:

Amerosporae: Spores one-celled, spherical, ovoid, or somewhat elongated.

Hyalosporae: spores hyaline.

Phaeosporae: spores colored some shade of light brown to black.

Didymosporae: Spores similar to the foregoing, but two-celled.

Hyalodidymae: spores hyaline.

Phaeodidymae: spores colored.

Phragmosporae: Spores three or more celled by transverse septa.

Hyalophragmiae: spores hyaline.

Phaeophragmiae: spores colored.

Dictyosporae: Spores divided by both transverse and longitudinal septa.

Hyalodictyae: spores hyaline.

Phaeodictyae: spores colored.

Scoleosporae: Spores very slender, thread or worm like, one-celled to several celled, hyaline or colored.

Helicosporae: Spores cylindrical and more or less spirally coiled, one celled to several celled, hyaline or colored.

Staurosporae: Spores radiately lobed or star or cross shaped, one celled to several celled, hyaline or colored.

This same scheme is used for other orders and families of Imperfect Fungi in which conidia are produced, with the omission of such subdivisions as are not represented. Where only a few forms are present in the major subdivisions the minor ones based on spore color are often omitted. In the discussion of representative genera of this class the group name, based on the foregoing scheme, follows the generic name in parenthesis.

The following genera should be mentioned: *Phyllosticta*, *Phoma* and *Macrophoma* (all Hyalosporae). Their 2500 or more species are parasitic on leaves and stems of plants. The first produces definite leaf spots, the other two produce less definite spots and occur on other parts of the host as well. *Macrophoma* as the genus is usually defined, but incorrectly, according to Petrak and Sydow, has large conidia, over 15 μ long, otherwise is like the others. The

pycnidium is buried in the host tissue but the short ostiole emerges at maturity. The distinctions between *Phyllosticta*, *Phoma* and *Macrophoma* are clearly entirely artificial. A leaf spot of the beet (*Beta vulgaris*) is caused by *Phyllosticta tabifica*. The same fungus on the roots and inflorescence has been called *Phoma betae*. Various species of these genera have been shown to have as their perfect stage species of *Guignardia*, *Mycosphaerella*, etc. in the Sphaeriales or Pseudosphaeriales. The specific distinctions have to a considerable extent been based on the host species attacked. Until very extensive inoculation experiments can be carried out this basis for segregation of species will probably continue to be used. *Cytospora* and *Ceuthospora* (Hyalosporae) produce their pycnidial cavities in subepidermal or subcortical stromata. The spores emerge from the separate or united ostioles in an amber colored cirrus. Many of the species are the imperfect stages of *Valsa* and related genera in the Sphaeriales. *Sphaeropsis* (Phaeosporae) corresponds to *Macrophoma* except that the conidia are dark colored. *S. malorum* causes twig cankers on apple and quince and the so-called black rot of the fruits. Its perfect stage is *Physalospora*. This genus is broken up by the more recent authors into several genera. The name *Sphaeropsis* having been first applied to the perfect stage of an Ascomycete should, according to Petrak and Sydow, be replaced by *Haplosporella*. Some of the species usually included here they transfer to *Botryodiplodia*, including among those so transferred *S. malorum*. *Coniothyrium* has smaller pycnidia and very much smaller conidia which emerge from the ostiole in a black cirrus. *Coniothyrium fuckelii*, the cause of the cane blight of various species of *Rubus*, has as its perfect stage *Leptosphaeria coniothyrium* in the Sphaeriales. *Ascochyta* (Hyalodidymae) is essentially a *Phoma* with two-celled conidia. *A. pisi* is very destructive to cultivated peas. Its perfect stage is *Mycosphaerella pinodes*. *Diplodia* (Phaeodidymae) is like *Macrophoma* with colored two-celled spores. In fact some species of *Diplodia* have been described as *Macrophoma*, *Sphaeropsis* and *Diplodia* depending upon the age of the conidia. Such species are placed by some authors in *Botryodiplodia*. All three types of spores may be present in the same pycnidium and all are viable. The 500 or more described species occur in leaves, stems, etc., and are often the cause of serious diseases of their hosts plants. *Septoria* (Scolecosporae) is a genus of over 1000 species, practically all parasites. Like *Phoma*

the pycnidium is immersed in the host tissue and the short ostiole projects to the surface (Figure 132). The conidia are long and slender, often considerably longer than the diameter of the pycnidium, hence curved within the latter. Two serious diseases of celery are caused by *S. apii* and *S. apii-graveolentis* respectively. *S. lycopersici* defoliates the older plants of tomato (*Lycopersicum*) and causes enormous losses. The perfect stage of some species of *Septoria* belongs to the genus *Mycosphaerella*.

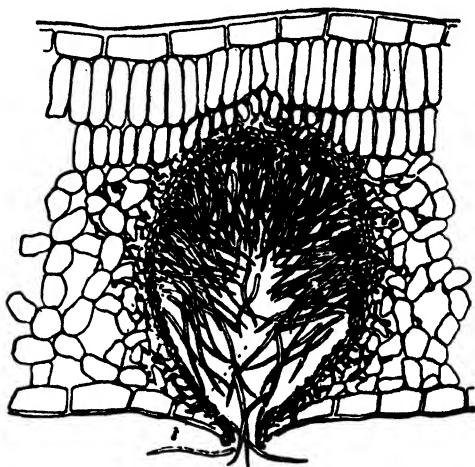


FIG. 132.—Sphaeropsidales. *Septoria pyricola*. (After Duggar, 1909.)

FAMILY ZYTHIACEAE (NECTRIOIDACEAE).—The pycnidia are bright colored and waxy, like the perithecia of the Hypocreales. Bender recognizes 62 genera. *Zythia* (Hyalosporae) is essentially a *Phoma* with bright colored pycnidia. Some species are parasitic. *Aschersonia* (Hyalosporae) produces its pycnidia buried in a bright colored stroma with several separate or united ostioles. The stroma is produced externally on leaves or twigs and in some, probably all, cases is parasitic upon insects feeding upon the supporting plant.

FAMILY LEPTOSTROMATACEAE.—The pycnidia have a well developed upper half but the basal portion is not well developed. They resemble in many respects the fruiting bodies of some of the Hemisphaeriales. Bender recognizes 88 genera. They are largely leaf-inhabiting saprophytes and parasites. *Leptothyrium pomi* (Hyalosporae) produces the so-called "fly-specks" of apple fruits.

These are the minute flattened round pycnidia. *Leptostroma* (Hyalosporae) produces elongated pycnidia with slit-like ostioles, on leaves, stems, etc. *Entomosporium maculatum* (Hyalophragmiae) forms four-celled conidia, the cells forming a sort of square, each with bristles. It causes leaf and fruit spots of the pear (*Pirus*). Its perfect stage is *Diplocarpon soraueri*, Family Mollisiaceae, Order Pezizales.

FAMILY EXCIPULACEAE.—The pycnidia early open out to a more or less deep, cup or saucer shaped structure, tough or hard and black, either arising subepidermally or subcortically and breaking through to the outside, or in some cases external from the first. Largely saprophytic on twigs, stems, etc., less often on leaves. It is sometimes difficult to distinguish certain subcortical species of this family from the following order (Melanconiales). Bender recognizes 59 genera. *Excipula* and *Discula* (Hyalosporae) and *Discella* (Hyalodidymae) are among the genera with the greatest number of species.

Order Melanconiales.—This order of 92* genera and over 600 North American species consists of but one family, MELANCONIACEAE. To a large extent the species are parasitic, causing the type of plant disease known as anthracnose. The three form genera *Gloeosporium*, *Colletotrichum* and *Myxosporium* (Hyalosporae) contain some of the most destructive parasites of cultivated plants. They differ by arbitrary characters. *Colletotrichum* (Figure 133, A) produces stiff colorless or colored bristles (setae) around the acervulus while these are lacking in the other two. *Gloeosporium* occurs on herbaceous host structures while *Myxosporium* occurs on woody stems. How artificial these distinctions are may be seen in the case of the fungus called *Colletotrichum gloeosporioides*, a common parasite of the leaves, young twigs and fruits of species of *Citrus* and many other genera. When inoculated upon the mango (*Mangifera indica*) setae are produced on some of the acervuli on the twigs and leaves but on the fruits the setae are lacking. Mr. G. L. Fawcett, then a colleague of the author, grew this fungus on over fifty different hosts in Miami, Florida. These had been described in literature under 25 or more species names in the two genera *Gloeosporium* and *Colletotrichum*. On many of these hosts the perfect stage was produced and was found to be *Glomerella cingulata*, of the Family

* The figures for this and the following orders and families are taken from H. B. Bender (Thesis, 1931).

Gnomoniaceae. Since it grows upon twigs as well as on the leaves and fruits the distinction between *Myxosporium* and *Gloeosporium* breaks down. The acervuli begin at first as a tangled subepidermal mass of hyphae from which arise numerous closely packed conidiophores which partially raise the epidermis. From the apex of each conidiophore are developed one or more conidia, embedded in gum. When moisture is abundant this gum swells and the epidermis is burst open and the spores are exuded in a sticky mass. Insects

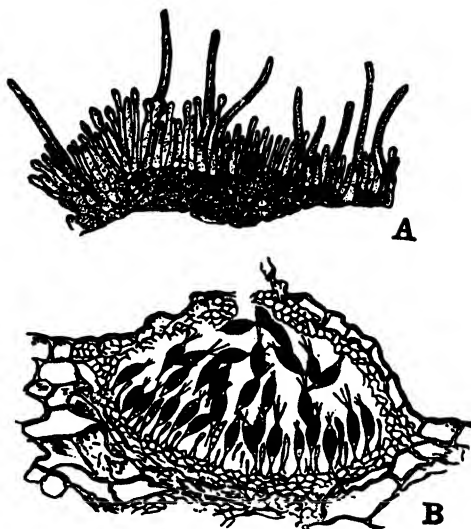


FIG. 133.—Melanconiales. A, *Colletotrichum malvarum*; B, *Pestalotia versicolor*. (A after Southworth, U.S.D.A., 1890; B, after Klebahn, 1913.)

or other objects coming into contact with these spores distribute them, as does rain, whose drops striking such a spore mass are broken up into smaller wind-borne droplets, each carrying its burden of spores. *Gloeosporium ribis* is the imperfect form of *Pseudopeziza ribis*, in Family Mollisiaceae, Order Pezizales. Some species of *Myxosporium* are imperfect stages of *Diaporthe* in the Sphaeriales. *Marssonina panattoniana* (Hyalodidymae) causes injury resulting in the formation of holes in leaves of lettuce (*Lactuca sativa*) and is sometimes very destructive in greenhouses. *Septogloeum* (Hyalophragmiae) is mostly parasitic on leaves. It resembles *Gloeosporium* with somewhat elongated, transversely septate spores. *Coryneum* (Phaeophragmiae) has numerous species. *C. beijerinckii* occurs in

Europe and various parts of the United States as the cause of a serious disease of the peach (*Amygdalus persica*). It kills twigs or may attack the buds and merely kill these and the surrounding tissues, or may cause injury to the fruit. The four or more-celled spores are dark colored and long stalked. *Pestalotia* (*Pestalozzia*) also has quite similar spores but the apical cell bears 1 to 3, rarely more, bristles (Figure 133, B). The terminal cells are lighter colored than the remaining ones. These are saprophytes on many hosts but some species are said to be destructive parasites. The perfect stages of these two genera are unknown. *Cylindrosporium* (Scolecosporae) causes leaf spots and leaf fall on many plants. The acervuli resemble those of *Gloeosporium* but the spore are long and slender. Perfect stages have been demonstrated for a few species. Thus those species attacking the genus *Prunus* have been shown to belong to the genus *Higginsia*, Family Mollisiaceae (often, but according to Nannfeldt erroneously, called *Coccomyces*).

Order Moniliales.—(**Hyphomyceteae**).—This order contains 651 genera and toward 10,000 species divided into four families. The first two are distinguished by the color of the mycelium and conidiophores. The older distinction included in the first family those genera with light colored or bright colored mycelium and conidiophores and conidia. Forms with dark colored mycelium and conidiophores were placed in the second family; whether the conidia were light or dark, as well as forms with light colored conidiophores but colored conidia. The author follows Bender in making the distinction as follows:

FAMILY MONILIACEAE.—Mycelium and conidiophores hyaline or bright colored, (not brown, smoky or black), conidia hyaline or colored. Conidia formed on the ends of short conidiophores not distinguishable from the other branches of the mycelium or terminal or lateral on distinct, unbranched or branched, separate conidiophores. In a few cases the mycelium breaks up into more or less rounded conidia. Saprophytes or parasites, including some of the most ubiquitous molds and some very serious enemies of economic plants. Bender recognizes 204 genera and over 500 North American species.

FAMILY DEMATIACEAE.—Like the foregoing except that the mycelium and conidiophores are dark. The conidia may be dark or light colored. 206 genera and over 1000 North American species.

FAMILY STILBACEAE.—In this family of 89 genera and about 100 North American species the mycelium spreads through the substratum in the usual manner but the rather long conidiophores arise together in a more or less compact column or synnema. At the top or down the sides the tips of the conidiophores spread apart and bear their spores. The degree of union is various so that the structure varies from a very short column and bushy head to a tall column with a small head.

FAMILY TUBERCULARIACEAE.—152 genera and over 400 North American species. In this family the conidiophores arise more or less radially, packed close together or separate, from the surface of a more or less rounded mass of hyphae forming a sort of cushion, or sporodochium. This may be hyphal in structure or pseudoparenchymatous and may be waxy, gelatinous or horny. The conidia are produced terminally or laterally from the unbranched or branched conidiophores. The sporodochium and conidia may be light colored or dark colored.

Among the many genera of the **MONILIACEAE** the following may be mentioned to show some of the various morphological types represented in the family: *Oospora* (Hyalosporae): mycelium very slender, unbranched or branched. Conidia formed by the breaking up of the mycelium into short cells which round up to form ellipsoidal or spherical, hyaline or light-colored conidia ("oidia"). *O. lactis* forms a thick wrinkled skin on sour milk and other liquids containing considerable organic matter. The genus *Actinomyces* should be sought here if it is regarded as a fungus and not one of the Bacteria. Its very slender, usually radiating mycelium is segmented into short rod-like cells of size comparable to that of bacteria. The presence of true nuclei is disputed. *A. bovis* is the cause of "lumpy jaw" of cattle and *A. scabies* causes scab of the tubers of potato (*Solanum tuberosum*). In *Cephalosporium* (Hyalosporae) the conidiophores are short and produce the spherical or ellipsoidal conidia successively at the apex, each new conidium pushing aside the last formed conidium, all of these sticking together by means of a small amount of slime, probably, and forming a head at the apex of the conidiophore. Some species are parasitic on fruiting bodies of *Polyporus*, etc. The microspores of some species of *Fusarium* are of this type. *Aspergillus* and *Penicillium* (both genera of Hyalosporae) include many species each, of which the perfect stages are known for a few

only, so that they must be considered among the Imperfect Fungi as well as among the Ascomyceteae. In *Aspergillus* the upright conidiophore is enlarged at the apex into a head from which arise short sterigmata bearing each a chain of approximately spherical conidia. These are produced successively at the apex of the sterigma so that the terminal conidium of the chain is the oldest. The conidia may be hyaline, yellow, green, ochre or even black (*Aspergillus niger*). In some species when grown with abundance of nutrients

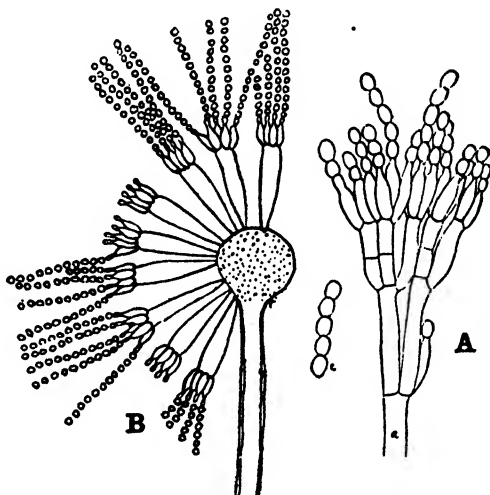


FIG. 134.—Moniliales. A, *Penicillium commune*; B, *Sterigmatocystis basidi-septa*. (A after Thom, 1930; B after Sartory, Sartory and Meyer, 1929.)

the sterigmata produce at their apices groups of secondary sterigmata which bear the conidial chains. Such species have been segregated as the genus *Sterigmatocystis* (Figure 134, B), but most of these in less rich media produce their conidia as in typical species of *Aspergillus*. In *Penicillium* (Figure 134, A) the conidiophore produces two or more branches which grow more or less parallel to the main filament and at about the same level produce several sterigmata each, with chains of conidia. These vary in color like those of *Aspergillus*. These fungi are mostly ubiquitous saprophytes, but one or two species of *Aspergillus* are parasitic in the human ear. *Botrytis* (Hyalosporae) of several hundred described species, has much branched conidiophores with spherical or ellipsoidal conidia produced singly but close together in groups at the ends of the

branches (Figure 135, B). *B. cinerea* which is a destructive parasite of many cultivated plants produces sclerotia which enable it to overwinter. This or closely similar forms have been described as the imperfect stage of *Sclerotinia fuckeliana* of the Order Pezizales. *Cephalothecium* (Hyalodidymae) produces a head of two-celled conidia at the apex of a tall straight conidiophore. The conidia are rather pear-shaped and the two cells are usually unequal in size.

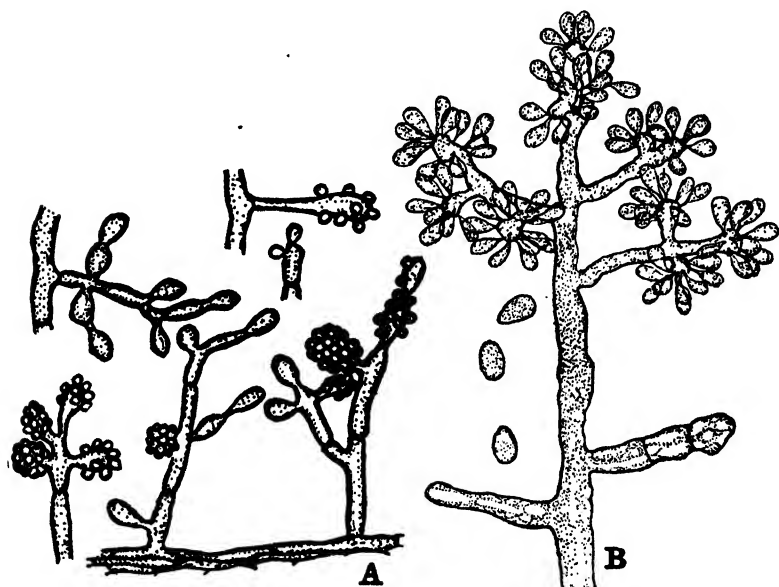


FIG. 135.—Moniliales. A, *Phymatotrichum omnivorum*; B, *Botrytis convoluta* (A after Duggar, 1916; B after Whetzel and Drayton, 1932.)

Singly they appear hyaline but in mass are pink. *Trichothecium* differs only in that the conidia are produced singly not in heads. Both are called “pink molds” and are saprophytes or wound parasites. *C. roseum* enters the fruit of the apple through the lesions caused by the scab fungus (*Venturia inaequalis*) and causes a storage rot. *Ramularia* (Hyalophragmiae) is parasitic on leaves and stems, producing typical leaf spots out of whose dead or dying tissues arise the stiff conidiophores which emerge through the stomata. The cylindrical, several celled, hyaline conidia are produced singly or in short chains. It should be noted that the conidia when produced in chains are produced acrogenously, i.e. the basal conidium of the

chain is the oldest and the apical conidium is the last one formed. They are at first one celled but usually before falling away become 2 or 3 septate. As they fall off they leave little scars on the conidiophore which grows on a very short distance and produces other conidia, and so on until the old conidiophore shows many such scars near its tip. Some species of *Ramularia* have been shown to be the imperfect stages of the genus *Mycosphaerella* in the Sphaeriales.

In the DEMATIACEAE many genera closely parallel those in the preceding family, differing in the dark color of the mycelium and conidiophores. More often the conidia are dark also. *Haplographium* (Phaeosporae) except for its dark-colored conidiophores and conidia closely resembles *Penicillium*. Its species are probably all saprophytic. *Polythrincium* (Phaeodidymae) produces its dark-colored twisted or wavy conidiophores in tufts emerging through the epidermis of the host leaf. They bear apically the colored two-spored conidia. *P. trifolii* is parasitic on the leaves of clover (*Trifolium*). *Cladosporium* (Phaeodidymae) with many hundred species, contains some undoubted parasitic species although many are saprophytic. The upright conidiophores bear laterally and terminally chains of conidia, which are produced acrogenously as in *Ramularia*. At first they are one-celled but the older conidia of the chain become once septate and sometimes two or three times septate. *C. cucumerinum* is the cause of the very destructive scab disease of the fruit of the cucumber (*Cucumis sativus*). *C. herbarum*, saprophytic on all sorts of dead vegetable matter and also described as sometimes parasitic, has been reported to have as its perfect stage a species of *Mycosphaerella* (Order Sphaeriales). *Helminthosporium* (Phaeophragmiae) produces its elongated, dark-colored smooth conidia at the apex of stiff, usually unbranched dark-colored conidiophores which emerge through the stomata or directly through the epidermis of the host leaf. The conidia are several celled by transverse septa and are uniform in thickness or slightly narrowed near the ends. Several species produce serious diseases of the small grains and wild grasses. The perfect stage of *H. teres* (Figure 69, A) has been determined to be *Pyrenophora teres*. Very similar to *Helminthosporium* is the genus *Heterosporium* which differs in its minutely warty or spiny conidia. These are produced one at a time, but the conidiophores produce several conidia successively as described above for *Ramularia*. *Heterosporium gracile*, the cause of a leaf

spot of various species of *Iris*, has for its perfect stage *Didymellina iridis*. *Macrosporium* and *Alternaria* (both Phaeodictyae) contain

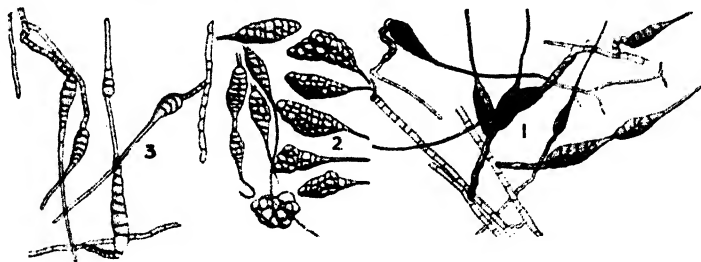


FIG. 136.—Moniliales. 1 and 2, *Alternaria brassicae* var. *nigrescens*; 3, *A. solani*. (After Elliott, 1917.)

saprophytic as well as parasitic species. The dark-colored conidiophores are short and stiff or somewhat elongated. The conidia are many septate transversely and many of the segments thus formed are divided by longitudinal septa. In *Macrosporium* the conidia are produced singly and in *Alternaria* in chains (Figure 136), the basal element of the chain being the oldest and best developed, the apical element being the last produced and smaller and not so completely septate. In a long chain the terminal conidium may be one-celled. The apical portion of each conidium of a chain is usually elongated to act, as it were, as a stipe for the conidium next above it. The chains break apart easily so that it is not always easy to distinguish the two genera. *A. brassicae* is injurious to leaves and other portions of cabbage and cauliflower (*Brassica* sp.), *A. brassicae* var. *nigrescens* causes a very serious "blight" of the muskmelon (*Cucumis melo*), *A. violae* causes a leaf spot of some varieties of the cultivated sweet violet (*Viola odorata*). A few species of *Alternaria* have as their perfect stage species of *Pleospora*. *Cercospora* (Scolecosporae) is possibly the most destructive genus in this family (Figure 137). Its many hundred species are all parasitic on leaves and sometimes on other green parts of as many or more species of higher plants. The short, stiff, dark-colored conidiophores emerge from the stomatal openings in tufts of varying number, from



FIG. 137.—Moniliales. *Cercospora rhapontici*, two conidiophores showing attachment scars, and a conidium. (After Tehon and Daniels, 1925.)

a pseudoparenchymatous mass of cells lying beneath the stoma and sometimes pushing up through it. As in *Ramularia* as soon as a conidium falls off another forms close to the scar left by it so that the

apical portion of an old conidiophore is crooked and marked by numerous scars. The conidia are long and slender, uniform in thickness or tapering gradually from the slightly thickened, rounded base. They may be hyaline or somewhat colored. They are transversely septate into many cells. *C. beticola* causes a very destructive leaf spot disease of beets, especially the sugar beet (*Beta vulgaris*). A leaf spot of cherry (*Prunus*) is caused by *C. cerasella*, the imperfect stage of *Mycosphaerella cerasella*.

In the STILBACEAE the genus *Stilbella* (Hyalosporae) produces its conidia only at the apex of the hyaline synnema, the conidia being one-celled and hyaline and produced singly, the whole head embedded in a drop of slime. In *Isaria* (Hyalosporae) the apices of the conidiophores grow out from the hyaline synnema for almost its whole length. The conidia are similar to those of *Stilbella* but are not borne in a slimy drop. The species of this genus are parasitic upon

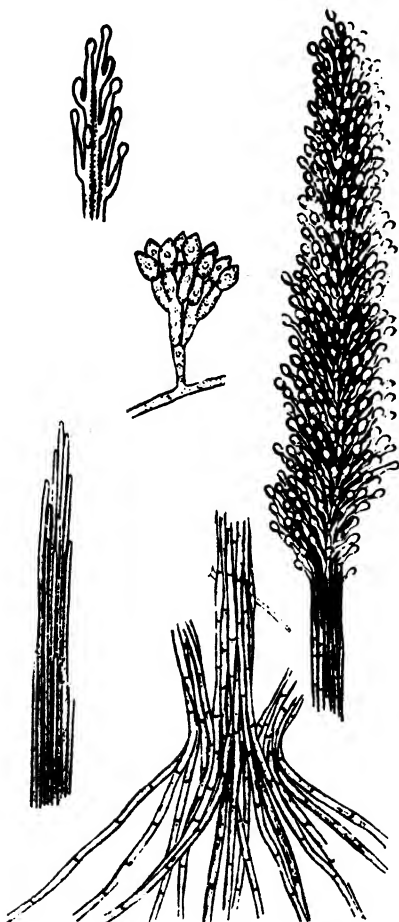


FIG. 138.—Moniliales, Stilbaceae. *Stysanus steimoniles*. (After Hasselbring, 1900.)

various insects. *Graphium* (Hyalosporae) corresponds to *Stilbella* except that the stalk of the synnema is dark colored. *G. ulmi*, the cause of the very destructive Graphium disease of the elm ("Dutch elm disease" so called because first observed in Holland),

is the imperfect stage of *Ceratostomella ulmi*. In *Stysanus* (Hyalosporae) the dark stalk bears an elongated head of conidiophores which produce the hyaline conidia in chains (Figure 138). Some species are parasitic.

THE FAMILY TUBERCULARIACEAE contains a variety of forms which are probably not closely related. The artificiality of the group is seen from the fact that the production or non-production of the sporodochium often depends upon the cultural conditions. Thus the author has grown *Colletotrichum gloeosporioides* so that it produced its normal acervuli, but in older drier cultures true sporodochia appeared. Later the latter enlarged and became thrown into folds and eventually became stromatic structures containing pycnidial cavities. Montemartini, in 1899, reported similar observations in several groups of Imperfect Fungi. *Tubercularia* (Hyalosporae) forms rounded, bright colored cushions, mostly on wood or bark. They are covered by fine, branching conidiophores bearing singly at the tips of the branches the small, elliptical hyaline conidia. *T. vulgaris* is the imperfect stage of *Nectria cinnabarina*. *Volutella* (Hyalosporae) produces its small, almost spherical sporodochia on the leaves or stems of herbaceous plants. Each sporodochium is surrounded by a circle of long bristles. The conidiophores are mostly unbranched. Several species cause diseases of plants. *V. dianthi* causes cankers near the base of the stem of the carnation (*Dianthus caryophyllinus*) which ultimately kill the plant. *Fusarium* (Hyalophragmiae) produces its usually lunate conidia (Figure 139) on rather broad, indefinitely bordered sporodochia as well as singly on the mycelium. The conidia are usually produced in a mass of slime and in mass may be white, yellow, orange or red in color. The many hundred species are distinguishable with difficulty, requiring to be cultured on a variety of culture media, under standard conditions of environment. In addition to this type of conidia (macrospores) there may be produced microspores which are single-celled conidia in heads (*Cephalosporium* type) as well as spores intermediate in character. Chlamydospores are often produced in abundance on the mycelium. Sometimes one or two are formed in a macrospore. Many species of *Fusarium* produce pigments which are of assistance in distinguishing the species. Among the species of this genus are many that cause wilt diseases; e.g. *F. lini* on flax (*Linum usitatissimum*), *F. oxysporum* on potato (*Solanum tuberosum*),

F. vasinfectum on cotton (*Gossypium*), etc. *Fusarium graminearum* causing the foot rot of maize (*Zea mays*) and scab of the heads of wheat and other small grains has been shown to be the imperfect stage of *Gibberella saubinetii* (Order Hypocreales). *Epicoccum* (Phaeosporae) forms little black dots on dead leaves and stems. These consist of short stout conidiophores radiating from small

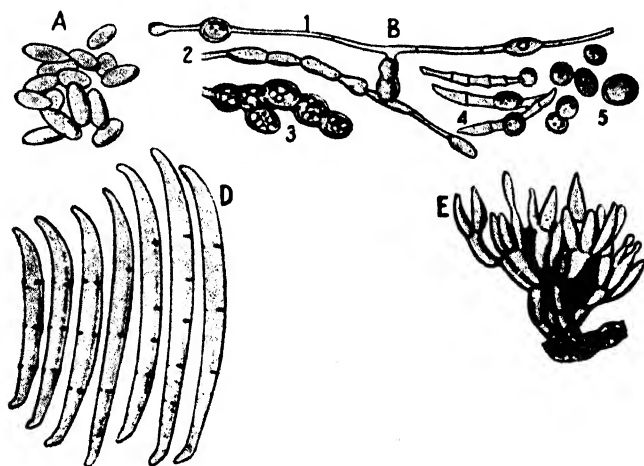


FIG. 139.—Moniliales. *Fusarium batatas*. A, microconidia; B, chlamydospores; D, macroconidia; E, conidiophore from sporodochium. (After Wollenweber in Jour. Agr. Res., 1914.)

black sporodochia. The dark one-celled conidia are spherical and slightly spiny or reticulately marked. *Exosporium* (Phaeophragmiae) forms similar sporodochia and very short conidiophores, but the conidia are elongated and have several transverse septa. Some species are doubtfully parasitic. *Spegazzinia* (Phaeodictyae or perhaps more properly Staurosporae) occurs on leaves, stems, and other plant debris and most species are probably saprophytic. The author has shown that two kinds of conidia are produced on the small black sporodochia. The commoner kind is very long stalked, the conidium consisting of four somewhat rounded spiny cells united at a common central point to which the conidiophore is attached. The second kind has very short conidiophores and the conidia are square, except for rounded corners, being divided into four cells by diagonal septa. They are smooth. The conidiophore is attached to the edge of one of the triangular cells making

up the conidium and arises directly from the sporodochium not, as described by some authors, from the long stalked conidia. The spiny conidia of the long-stalked type germinate by bladder-like outgrowths from which radiate many germ tubes: the smaller type of conidium germinates by a single germ tube from each cell of the conidium.

Order Mycelia Sterilia.—Twenty genera and 400 or more species. This exceedingly heterogeneous group is not at all a coherent assemblage of related species. Any non-sporiferous mycelial structure, whether sclerotium, rhizomorph, dense or loose mass of mycelium etc., is placed here. The presence of clamp connections in some species shows that these forms belong to the Class Basidiomyceteae, their absence in very many cases may or may not indicate that these belong elsewhere. The form genus *Sclerotium* includes species producing sclerotia with more or less definite form, usually light-colored internally and with a brown or black rind. For many forms only the sclerotia and associated mycelium are known, but many similar sclerotia produce apothecia (*Sclerotinia* in the Pezizales) or Basidiomycetous spore-fruits (*Typhula* in the Family Clavariaceae), etc. *Pachyma* is an enormous subterranean sclerotium, more or less fibrous fleshy internally and rough or irregular externally. *P. cocos* sometimes is larger than a man's head and was formerly used for food by the Indians inhabiting the regions now comprised by Virginia and adjacent states. Its perfect stage is a species of *Polyporus* which grows out of the sclerotium. *Rhizoctonia* consists of superficial, irregular, scale-like, black sclerotia growing on the surface of the subterranean portion of the host plant, these being preceded and accompanied by a superficial dark-colored, short celled, abundantly branching rather stout mycelium. This mycelium is entirely different in appearance from the slender, hyaline mycelium growing within the host tissues. The perfect stage of *Rhizoctonia solani* is *Corticium vagum*, Family Thelephoraceae. It is a very destructive enemy of many species of cultivated plants such as potato (*Solanum tuberosum*), bean (*Phaseolus vulgaris*), sugar beet (*Beta vulgaris*) as well as of a host of wild plants. *Rhizomorpha* is the name given to strands of mycelium, dark externally and usually white internally. *R. subcorticalis* consists of the rhizomorphs of *Armillaria mellea* (Family Agaricaceae). *Ozonium* consists of loose masses of usually bright colored mycelium fre-

quently uniting into strands and again spreading out. Some species are parasitic, others saprophytic. *O. omnivorum*, destructive to cotton (*Gossypium*) and many other cultivated as well as wild plants in Texas and adjacent states, spreads through the soil and attacks the roots of the host plants. It sometimes produces a conidial stage, *Phymatotrichum omnivorum* (Family Moniliaceae, Figure 135, A) and possibly has as its perfect stage a species of *Hydnum* (Family Hydnaceae) which has been found associated with it. Many other forms of mycelium have been given names but hardly deserve discussion here.

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Contains an explanation of the arrangement of genera by spore form and color.

CHAPTER XV

GUIDE TO THE LITERATURE FOR THE IDENTIFICATION OF FUNGI

The vast number of fungi makes a knowledge of even a considerable part of the species beyond the ability of all but a few specialists. To be able to identify a given specimen requires that the necessary literature be available. Before 1880 the great Italian mycologist, P. A. Saccardo, began to work on a compilation of all species of fungi described up to that time. These descriptions were brought together in a compendious work entitled *Sylloge Fungorum*, of which the first volume appeared in 1882. The descriptions, in Latin, were arranged in accordance with the systematic classification of fungi then recognized by the author. He completed the work with Volume VIII in 1889, but in the mean time, such was the stimulus afforded by this great work, bringing together in one place all known species of fungi, that thousands of additional species were recognized and described. Thus it became necessary to publish supplementary volumes, the last of which, Volume XXV, appeared in 1931. For the last twenty years species of fungi have been described at the rate of 1500 to 2500 species a year. Thus it is inevitable that such a work must be from two to five years behindhand. A further difficulty is the language of the description, Latin, a knowledge of which is unfortunately all too meagre among the later generation of botanists. Furthermore the lack of illustrations and the necessary scattering of the descriptions among the original volumes and the many supplements make the work difficult to use. Besides this, the necessarily high cost precludes its purchase by most botanists so that they must depend upon the copies owned by libraries.

To obviate these difficulties local fungus floras have been issued in various countries or even subdivisions of countries. These publications are usually in the language of the country and are

furthermore smaller, inasmuch as only the species occurring in the limited areas concerned are included.

Still another type of publication is the monograph, or intensive study of some smaller group of fungi, such as a family or a genus or even a section of a genus. By virtue of the limitation of effort to this relatively small number of species it is possible for such a monograph to devote larger space to the description of the individual species and to make their identification more easy.

In the following pages the more general works are first listed; then under different headings are included the publications that are confined more to special groups. These are arranged systematically in accordance with the classification of the fungi. It is the aim of the author to list the more recent publications of this nature from all parts of the world, but it is certain that there are many omissions, especially for parts of the world whose mycological literature is not so widely available in the United States as is the literature of this country and of the larger European countries. Even for the latter the large number of publications from botanical or mycological societies of somewhat limited scope makes a complete list difficult to obtain as in no one library will even a majority of such works be found.

The student is advised to turn first to the portion of the list where these papers of monographic nature are to be found. In case no such paper is listed for the fungus he has he must turn to the more general lists.

Because of the various systems of classification used by different authors the arrangements of the items in the following list does not follow any one system in all its details. Cross references are necessary in the cases where one work includes groups now segregated although formerly united.

It must be remembered that certainty of identification depends not only upon the availability of the necessary literature but also upon the fullness of the knowledge of the structure, development, etc. of the fungus in question. The literature should not be consulted until the main morphological and anatomical details have been ascertained, including measurements of spores, sporophores, etc. The fuller the details are known as to the substratum on which the fungus grows, its habitat, color, appearance when fresh, appearance

at different stages of development, etc., the more easily will the identification be effected.

I. GENERAL WORKS COVERING THE WHOLE FIELD OF SYSTEMATIC MYCOLOGY

SACCARDO, P. A. *Sylloge fungorum omnium hucusque cognitorum*. Twenty-five volumes issued up to 1931. Pavia, Italy.

- 1: 1-768. 1882. Pyrenomycetaceae.
- 2: 1-959. 1883. Pyrenomycetaceae (cont.).
- 3: 1-860. 1884. Sphaeropsideae and Melanconieae.
- 4: 1-807. 1886. Hyphomycetaceae.
- 5: 1-1146. 1887. Hymenomycetaceae I. Agaricineae.
- 6: 1-928. 1888. Hymenomycetaceae II. Polyporeae, Hydneae, Thelephoreae, Clavariaceae, Tremellineae.
- 7: 1-941. 1888. Gasteromycetaceae, Phycomycetaceae, Myxomycetaceae, Ustilagineae, Uredineae.
- 8: 1-1143. 1889. Discomycetaceae, Phymatosphaeriaceae, Tuberaceae, Elaphomycetaceae, Onygenaceae, Laboulbeniaceae, Saccharomycetaceae, Schizomycetaceae.
- 9: 1-1141. 1891. Supplement 1. Hymenomycetaceae, Gasteromycetaceae, Hypodermeae (Ustilaginaceae and Uredinaceae), Phycomycetaceae, Pyrenomycetaceae, Laboulbeniaceae.
- 10: 1-964. 1892. Supplement 2. Discomycetaceae, Onygenaceae, Tuberoideae, Myxomycetaceae, Sphaeropsideae, Melanconieae, Hyphomycetaceae, Fossil Fungi.
- 11: 1-753. 1895. Supplement 3. All groups of fungi. Generic index to all volumes.
- 12: 1-1053. 1897. Index to first eleven volumes.
- 13: 1-1340. 1898. Host Index.
- 14: 1-1316. 1899. Supplement 4. All groups of Fungi. Sterile Mycelia.
- 15: 1-455. 1901. Supplement 5. Synonyms.
- 16: 1-1291. 1902. Supplement 6. All groups of Fungi. Generic index to all volumes.
- 17: 1-991. 1905. Supplement 7. Hymenomycetaceae, Gasteromycetaceae, Uredinaceae, Ustilaginaceae, Phycomycetaceae, Pyrenomycetaceae, Laboulbeniomycetaceae.
- 18: 1-838. 1906. Supplement 8. Discomycetaceae (including Saccharomycetaceae, Exoascaceae, Gymnoascaceae, Tuberaceae, etc.), Myxomycetaceae, Deuteromycetaceae (= Fungi Imperfecti). Generic index for all volumes.
- 19: 1-1158. 1910. Index of Illustrations of Fungi, A-L.
- 20: 1-1310. 1911. Index of Illustrations of Fungi, M-Z.
- 21: 1-928. 1912. Supplement 9. Hymenomycetaceae, Gasteromycetaceae, Ustilaginaceae, Uredinaceae, Phycomycetaceae.
- 22: 1-612. 1913. Supplement 10. Ascomycetaceae, Deuteromycetaceae, Sterile Mycelia.

- 23: 1-1026. 1925. Supplement 10, continued. Hymenomyceteae, Ustilaginales, Uredinales.
- 24, Section I: 1-703. 1926. Supplement 10, continued. Phycomyceteae, Laboulbeniales, Pyrenomyceteae, in part.
- 24, Section II: 704-1438. 1928. Supplement 10, continued. Remainder of Pyrenomyceteae, Discomyceteae, Appendix, consisting of additions to Vols. 23 and 24.
- 25: 1-1093. 1931. Supplement 10, continued. Myxomyceteae, Myxobacteriaceae, Deuteromyceteae, Mycelia Sterilia.
- Volumes 1, 10 and 17 contain bibliographies; Vol. 14 contains an explanation of the arrangement of genera by the spore form and color scheme.
- ENGLER, A. und K. PRANTL. *Die natürlichen Pflanzenfamilien*. Wilhelm Engelmann. Leipzig. The parts devoted to fungi (including the Lichens) are the following:
- I. Teil, Abteilung 1: 1-513. *Figs. 1-293*. 1897.
Myxomyceteae, Phycomyceteae, Ascomyceteae.
- I. Teil, Abteilung 1*: 1-249. *Figs. 1-125*. 1907.
Lichens.
- I. Teil, Abteilung 1**: 1-570. *Figs. 1-263*. 1900.
Basidiomyceteae, including Hemibasidii (Ustilaginales) and Uredinales.
Fungi Imperfecti.
- This work will enable one to determine the genus of almost any fungus but not the species. It is very helpful because of the illustrations.
- ENGLER, A. und K. PRANTL. *Die natürlichen Pflanzenfamilien*. Wilhelm Engelmann, Leipzig. Zweite Auflage.
- 2: 304-339. *Figs. 425-447*. 1928.
Mycetozoa.
- 6: 1-290. *Pls. 1-5. Figs. 1-157*. 1928.
Ustilaginales, Uredinales. Hymenomyceteae.
- 7a: 1-122. *Figs. 1-91*. 1933.
Gastromyceteae.
- 8: 1-270. *Figs. 1-127*. 1926.
Lichens.
- CLEMENTS, FREDERICK E. and CORNELIUS L. SHEAR. *The genera of fungi*. iv + 496 pp. 58 pls. H. W. Wilson Company, New York. 1931.
- RABENHORST, L. *Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz*. Zweite Auflage. Verlag von Eduard Kummer. Leipzig.
- Band 1. WINTER, GEORG. *Die Pilze*. This "Volume" on Fungi is so extensive that it is issued as ten separately bound "Abteilungen," as follows:
- 1: 1-924. 1 plate and numerous text figures. 1884. Schizomyceten, Saccharomyceten, und Basidiomyceten. By A. DE BARY, H. REHM, and GEORG WINTER.
- 2: 1-928 and Index, 1-112. Numerous text figures. 1887.
Ascomyceten: Gymnoasceen und Pyrenomyceten. By A. DE BARY, H. REHM, and GEORG WINTER.
- 3: 1-1275 and Index, 115-169. Numerous text figures. 1896.
Ascomyceten: Hysteriaceen und Discomyceten. By H. REHM.

- 4: 1-505. *Figs. 1-74.* 1892.

Phycomyceten. By ALFRED FISCHER.

- 5: 1-131. *Numerous text figures.* 1897.

Ascomyceten: Tuberaceen und Hemiasceen. By EDUARD FISCHER.

- 6: 1-1016. *Numerous text figures.* 1901.

Fungi Imperfecti: Hyalin-sporige Sphaerioideen. By ANDREAS ALLESCHER.

- 7: 1-993. Index to Abteilungen 6 + 7, pp. 995-1072. *Numerous text figures.* 1903.

Fungi Imperfecti: Gefärbt-sporige Sphaerioideen, sowie Nectrioideen, Leptostromaceen, Excipulaceen und Melanconieen. By ANDREAS ALLESCHER.

- 8: 1-852. *Numerous text figures.* 1907.

Fungi Imperfecti: Hyphomyceten; Mucedinaceen und Dematiaceen (Phaeosporae und Phaeodidymae). By G. LINDAU.

- 9: 1-983. *Numerous text figures.* 1910.

Fungi Imperfecti: Dematiaceen (Phaeophragmiae bis Phaeostauroporae), Stilbaceen und Tuberculariaceen. By G. LINDAU.

- 10: 1-474. *182 figs.* 1920.

Myxogasteres (Myxomycetes, Mycetozoa). By HANS SCHINZ.

- Band 8. KEISSLER, KARL VON. *Die Flechtenparasiten.* xi + 712 pp. 135 figs. 1930.

- Band 9. ZAHLEBRUCKNER, ALEXANDER. *Die Flechten (Lichenes).* So far only the following Abteilungen have appeared:

- 1, Teil 1: 1-480. 261 figs. 1933.

Moriolaceen by KARL VON KEISSLER; Verrucariaceen und Dermato-carpaceen, by H. ZSCHACKE.

- 4, Teil 1: 1-426. 8 pls. 64 figs. 1933.

Cladoniaceen (except Cladonia), by E. FREY.

- Teil 2: 1-531. 34 pls. 8 figs. 1931.

Cladonia by H. SANDSTEDE.

Kryptogamenflora der Mark Brandenburg.

Gebrüder Borntraeger, Leipzig.

This work appears in nine or more volumes of which the following concern the fungi.

5. 630 pp. 151 figs. 1915. Schizomycetes, by R. KOLKWITZ; Myxobacterales, by E. JAHN; Chytridiineae, Ancylistineae, Monoblepharidineae, Saprolegniineae, by M. VON MINDEN.

- 5a. 946 pp. 380 figs. 1914. Uredineen, by H. KLEBAHN; Ustilagineen, Auriculariineen, Tremellineen, by G. LINDAU.

6. Not complete. Issued so far only

- Heft 1: 1-92. *Many illustrations.* 1910. By W. HERTER.

Autobasidiomycetes: Dacryomycetaceae, Exobasidiaceae, Tulasnellaceae, Corticiaceae, Thelephoraceae, Cyphellaceae, Craterellaceae, Clavariaceae, Sparassiacae, Hydnaceae (incomplete).

7. Not complete. Issued so far only
 Heft 1: 1-160. *Many illustrations.* 1905.
 Hemiasci, by G. LINDAU; Saccharomycetinae, by P. LINDNER; Protoascineae, by G. LINDAU; Exoascaceae, by F. NEGER; Ascocorticiaceae and Gymnoascaceae, by G. LINDAU; Aspergillaceae, by F. NEGER; Onygenaceae, Elaphomycetaceae and Terfezaceae, by P. HENNINGS; Erysiphaceae and Perisporiaceae, by F. NEGER; Tuberaceae (incomplete) by P. HENNINGS.
 Heft 2: 161-304. *Many illustrations.* 1911.
 Tuberaceae (completed), by P. HENNINGS; various families of the Sphaeriales, by W. KIRSCHSTEIN.
8. No parts yet issued.
9. 962 pp. 339 figs. 1915. Sphaeropsideen, Melanconien, by H. DIEDICKE.
 OUDEMANS, C. A. J. A. *Révision des Champignons tant supérieurs qu'inférieurs jusqu'à ce jour trouvés dans les Pays-Bas.*
 1: 1-638. 1893. Hymenomycetes, Gasteromycetes, Hypodermeae.
 2: 1-491. Pls. 1-14. 1897. Phycomycetes and Pyrenomycetes.
 SCHROETER, J. *Die Pilze Schlesiens.*
 COHN's Kryptogamen-Flora von Schlesien 3. J. V. KERN's Verlag. Breslau.
 Erste Hälfte. 1-814. 1889. Myxomycetes, Schizomycetes, Chytridiei, Zygomycetes, Oomycetes, Protomycetes, Ustilaginei, Uredinei, Auriculariei, Basidiomycetes. Host index for this half volume.
 Zweite Hälfte. 1-597. 1908. Ascomycetes and a small part of the Fungi Imperfecti. Host index for second half volume.
- MIGULA, W. *Kryptogamen-Flora von Deutschland, Deutsch-Österreich und der Schweiz.* Teil 2 of Thomé. Flora von Deutschland etc. Zweite Auflage. Friedrich von Zetzschwitz. Gera.
 Band 3. Teil 1. IV + 510 pp. 92 pls. 1910.
 Myxomycetes, Phycomycetes, Basidiomycetes (Ordnungen Ustilagineae und Uredineae).
 Teil 2. IV + 814 pp. 304 pls. 1912.
 Basidiomycetes.
 Teil 3. Abteilung 1. IV + 1-684. Pls. 1-100. 1913.
 Hemiasci, Saccharomycetinae, Protodiscineae, Plectascineae, Pyrenomycetes (Perisporiales und Sphaeriales).
 Teil 3. Abteilung 2. IV + 685-1404. Pls. 101-200. 1913.
 Dothideales, Hypocreales, Hysteriales, Discomycetes, Laboulbeniaceae.
 Teil 4. Abteilung 1. IV + 614 pp. 90 pls. 1921.
 Fungi Imperfecti.
- Band 4. Teil 1. VIII + 527 pp. 82 pls. 1929.
 Teil 2. IV + 868 pp. 143 pls. 1931.
 Flechten.
- JACZEWSKI, A. A. *Identification of fungi* (Russian).
 Vol. 1, 1913. Vol. 2, 1917.
- JACZEWSKI, A. A. and P. A. *Identification of fungi. Perfect forms (diploid stages).*
 Tom I. Phycomycetes. Third edition 294 pp. 329 figs. Leningrad and Moscow. 1931. [Russian.]

- COOKE, M. C. *Handbook of British Fungi with full descriptions of all the species and illustrations of the genera.* 2 vols. ii + 981 pp. 7 pls. 408 figs. Macmillan and Co. London. 1871. 2d. edition, 1883.
- MASSEE, GEORGE. *British fungus flora, a classified text-book of mycology.* George Bell and Sons, London.
- Vol. 1. xii + 432 pp. *Illustrated.* 1892. Gastromycetes; Tremellineae; Clavariaceae; Thelephoreae; Hydneae; Polyporeae; Agaricineae; Melanosporeae and Porphyrosporeae.
- Vol. 2. vii + 460 pp. *Illustrated.* 1893. Agaricineae; Ochrosporeae, Rhodosporeae, Leucosporeae.
- Vol. 3. viii + 512. *Illustrated.* 1893. Agaricineae; Leucosporeae; Hyphomycetes.
- Vol. 4. viii + 522 pp. *Illustrated.* 1895. Ascomycetes.
- . *British fungi with a chapter on Lichens.* 551 pp. *Colored Plates* 1-40. *Pls. A. and B.* 19 unnumbered figures. George Routledge and Sons, London. Undated, (about 1911).
- MASSEE, GEORGE and IVY. *Mildew, Rusts and Smuts: A synopsis of the Families Peronosporaceae, Erysiphaceae, Uredinaceae and Ustilaginaceae.* 229 pp. *Pls. 1-5.* Dulau and Co., London.
- CORDA, A. C. I. *Icones fungorum hucusque cognitorum.* J. G. Calve (Vols. 1-4), Fr. Ehrlich (Vols. 5-6). Prag.
- 1: 1-32. *Pls. 1-7.* 1837. Mostly Fungi Imperfecti; a few Uredinales, Mycetozoa and miscellaneous fungi.
- 2: 1-43. *Pls. 8-15.* 1838. Fungi Imperfecti, Mucorales, Mycetozoa, a few Uredinales, Ustilaginales, Pezizales and miscellaneous fungi.
- 3: 1-55. *Pls. 1-9.* 1839. Uredinales, Fungi Imperfecti, Agaricales, miscellaneous.
- 4: 1-53. *Pls. 1-10.* 1840. Erineum galls, Fungi Imperfecti, Uredinales, Mycetozoa, Agaricales and various Ascomyceteae.
- 5: 1-92. *Pls. 1-10.* 1842. Erineum galls, Fungi Imperfecti, Mucorales, Mycetozoa, Gasteromycetes, Tuberales, Agaricales and miscellaneous.
- 6: I-XIX, 1-91. *Pls. 1-20.* 1854. (Plates by CORDA, text by J. B. ZOBEL). Uredinales, Fungi Imperfecti, Mucorales, Mycetozoa, Gasteromycetes, Tuberales, Miscellaneous.
- JUILLARD-HARTMANN, G. *Iconographie des champignons supérieurs.* 5 vols. 250 colored plates. Juillard et Fils. Epinal. 1919 (for Vol. 1, others not dated).
- Illustrations in color of approximately 2400 species of fungi. Vols. 1-3 and part of 4 represent Agaricaceae, the remainder of Vol. 4 illustrates Polyporaceae, Boletaceae, Fistulinaceae; Vol. 5 illustrates Hydneae, Clavariaceae, Thelephoraceae, Exobasidiaceae, Gastromyceteae, Dacryomycetales, Tremellales, Auriculariales, Helvellaceae and a few subterranean Ascomyceteae. No descriptions accompany the plates.
- KONRAD, P. et A. MAUBLANC. *Icones selectae fungorum.* 10 fascicules to include 500 plates, of which six fascicules with 192 pages of text and 300 colored plates appeared between 1924-1930. Paul Lechevalier. Paris.

BRESADOLA, J. *Fungi Tridentini novi vel nondum delineati, descripti et iconibus illustrati*. Trieste.

1: 1-114. *Pls.* 1-105. 1881.

2: 118 pp. *Pls.* 106-217. 1892.

———. *Iconographia mycologica*, edited by J. TRAVERSO, L. FENAROLI, G. CATONI and J. B. TRAVERSO. 24 volumes, 1200 plates. Milan. 1927-32. Vols. 1-18, Agaricaceae; 19-21, Polyporaceae and part of Hydnaceae; 22, remainder of Hydnaceae, Thelephoraceae, part of Clavariaceae; 23, Clavaria, Auriculariaceae, Tremellaceae, Dacryomycetaceae, Gastromycetaceae; 24, Helvellaceae, Leotiaceae, Pezizaceae.

COUPIN, HENRI. *Album général des Cryptogames. Fungi (Champignons)*.

Les Champignons du Globe. 5 volumes. 473 plates. E. Orlhac. Paris. [About 1920-1925.] Gives illustrations of nearly all the recognized genera of fungi except the lichens.

SCHWARZE, CARL A. *The parasitic fungi of New Jersey*.

New Jersey Agricultural Experiment Station Bulletin 313: 1-226. *Figs.* 1-1056. 1917.

Contains beautiful illustrations of very many genera and species of parasitic fungi.

STEVENS, F. L. *The Fungi which cause Plant Disease*. ix + 754 pp. 449 figs. Macmillan, New York. 1913.

North American Flora, published by the New York Botanical Garden, New York.

Of this work various parts describing fungi have been issued, as follows:

Volume 3. Part 1. 1910. Hypocreales and Fimietariales.

Volume 6. Part 1. 1922. Phyllostictales (part).

Volume 7. Parts 1-13. 1906-1931. Ustilaginales and Uredinales.

Volume 9: 1-542. 1907-1916. Polyporaceae (part), Boletaceae, Agaricaceae (part).

Volume 10. Parts 1-5. 1917-1932. Agaricaceae (continued).

LARSEN, P. *Fungi of Iceland*, being Volume 2, part 3 of Rosenvinge, L. KOLDERUP and E. WARMING. *The Botany of Iceland*. Copenhagen and London. 1932.

II. HOST INDEXES, BIBLIOGRAPHIES AND MISCELLANEOUS

OUDEMANS, C. A. J. A. *Enumeratio systematica fungorum*. Martin Nijhoff. The Hague.

1: cxxvi + 1230 pp. 1919. Host index of Algae, Fungi, Bryophyta, Pteridophyta, Gymnosperms and Monocotyledons.

2: xix + 1069 pp. 1920. Dicotyledons: Salicaceae—Basellaceae.

3: xvi + 1313 pp. 1921. Dicotyledons: Caryophyllaceae—Vitaceae.

4: xiii + 1231 pp. 1923. Dicotyledons: Elaeocarpaceae—Compositae. Supplement.

5: vii + 999 pp. 1924. Index to species of hosts and fungi in Volumes 1-4.

This is a host index of all parasitic fungi reported in any part of the world on plants native to Europe or introduced into Europe.

SEYMOUR, ARTHUR BLISS. *Host Index of the Fungi of North America*. xiii + 732 pp. Harvard University Press, Cambridge. 1929.

COONS, G. H. *A preliminary host index of the fungi of Michigan, exclusive of the Basidiomycetes, and of the plant diseases of bacterial and physiological origin.*

Michigan Academy of Science Report 14: 232-276. 1912.

BISBY, G. R., A. H. REGINALD BULLER and JOHN DEARNESS. *The Fungi of Manitoba.* xii + 194 pp. 1 map. Longmans, Green and Co., New York and London. 1929.

Complete host indexes to the parasitic fungi, etc. Spore sizes given for the Fungi Imperfecti.

GILMAN, JOSEPH C. and W. ANDREW ARCHER. *The fungi of Iowa parasitic on plants.*

Iowa State College Journal of Science 3 (4): 299-507. 2 figs. 1929.

DAVIS, J. J. *A Provisional list of the parasitic fungi of Wisconsin.*

Transactions of the Wisconsin Academy of Sciences, Arts and Letters 17: 846-984. Oct. 1914.

Contains a host index for plant diseases in Wisconsin.

PETCH, T. *A list of the entomogenous fungi of Great Britain.*

Transactions of the British Mycological Society 17 (3): 170-178. 1932.

A list with hosts and localities of all entomogenous fungi known to occur in Great Britain with the exception of the Laboulbeniales.

VANIN, S. I. *Tables for the identification of house fungi (Russian).*

Materialy po Mikologii i Fitopatologii 2: 58-75. 1926.

LINDAU, G. et P. SYDOW. *Thesaurus litteraturae mycologicae et lichenologicae.* Gebrüder Borntraeger, Leipzig.

1: 1-903. 1908. Authors A. to L., up to 1906, incl.

2: 1-808. 1909. Authors M. to Z., up to 1906, incl.

3: 1-766. 1913. Corrections and additions up to 1910, incl.

4: 1-609. 1915. Subject lists. Applied mycology, geographical distribution, pathology.

5: 1-526. 1917. Subject lists continued. Systematically arranged.

A nearly complete bibliography of all mycological literature up to the close of 1910, arranged alphabetically by the authors. Vols. 4 and 5 are arranged by subjects, the plant diseases under their hosts.

VOUAUX, L'ABBÉ. *Synopsis des champignons parasites des lichens.*

Bulletin de la Société Mycologique de France 28: 177-256. 1912; 29: 33-128, 399-494. 1913; 30: 135-198, 281-329. 1914.

OTA, MASAO et MAURICE LANGERON. *Nouvelle classification des Dermatophytes.* Annales de Parasitologie 1 (4): 305-336. Figs. 1-8. 1923.

VUILLEMIN, PAUL. *Les champignons parasites et les mycoses de l'homme.*

Encyclopédie Mycologique 2: 1-290. Figs. 1-140. Paul Lechevalier et Fils. Paris. 1931.

SARTORY, A. *Champignons parasites de l'homme et des animaux.* 895 + 47 pp. 50 pls. 91 figs. Lefrançois. Paris. 1920.

GUBA, E. F. and P. A. YOUNG. *Check list of important references dealing with the taxonomy of fungi.*

Transactions of the American Microscopical Society 43: 17-67. 1924.

III. MYCETOZOA, PLASMIDIOPHORALES, ACRASIALES AND LABYRINTHULALES

- LISTER, ARTHUR. *A monograph of the Mycetozoa*. Third edition, revised by GULIELMA LISTER. xxxii + 296 pp. 222 pls. 60 figs. Trustees of the British Museum, London. 1925.
- MACBRIDE, THOMAS H. and G. W. MARTIN. *The Myxomycetes, a descriptive list of the known species with special reference to those occurring in North America*. 339 pp. 20 pls. Macmillan Co. New York. 1934.
- TORREND, C. *Flore des Myxomycètes*. 271 pp. 9 pls. 1908.
Reprinted from Broteria.
- JACZEWSKI, ARTHUR LOUIS. *Mycological Flora of European and Asiatic Russia*. II. *Myxomycetes* (Russian).
Materialien zur Kenntnis der Fauna und Flora des Russischen Reiches. Botanischer Teil. Heft 6: 1-140. 84 figs. 1907.
- YOSHIKADZU, EMOTO. *Die Myxomyceten Japans*. (Japanese)
Botanical Magazine (Tokyo) 48 (568): 279-287, (569): 342-353, (570): 408-417. Illustrated. 1934. (Further parts to follow.)
- GREENE, H. C. *Wisconsin Myxomycetes*.
Transactions of the Wisconsin Academy of Sciences, Arts and Letters 27: 141-181. 6 pls. 1932.
- COOK, W. R. IVIMEY. *A monograph of the Plasmodiophorales*.
Archiv für Protistenkunde 80 (2): 179-254. Pls. 5-11. Figs. 1-14. 1933.
- . *The parasitic slime-moulds*.
Hong Kong Naturalist Supplement 1: 29-39. Pls. 13-18. 1 Fig. Oct. 1932.
- OLIVE, EDGAR W. *Monograph of the Acrasidae*.
Proceedings of the Boston Society of Natural History 30: 451-513. Pls. 5-8. 1902.
- . *A preliminary enumeration of the Sorophoreae*.
Proceedings of the American Academy of Arts and Sciences 37: 333-344. 1901.
- The Acrasiales and Labyrinthulales make up this group called "Sorophoreae."
- DANGEARD, P. A. *Observations sur la famille des Labyrinthulales et sur quelques autres parasites du Cladophora*.
Le Botaniste 24 (3-4): 217-258. Pls. 22-24. Fig. 1. 1932.

IV. CHYTRIDIALES

- FITZPATRICK, HARRY K. *The lower fungi. Phycomycetes*. xi + 331 pp. Figs. 1-112. McGraw-Hill Book Co., New York. 1930.
- MINDEN, M. VON. *Chytridiineae, Ancylistineae, Monoblepharidineae, Saprolegniineae*.
Kryptogamenflora der Mark Brandenburg 5: 209-630. 1911-15.
- PETERSEN, H. E. *Contributions à la connaissance des Phycomycètes marins (Chytridiineae Fischer)*.

- Oversigt over Kongelige Danske Videnskabernes Selskab Forhandlingar
1905: 439-488. *Illustrated*. 1905.
- SCHERFFEL, A. *Einiges über neue oder ungenügend bekannte Chytridiceen.*
Beiträge zur Kenntnis der Chytridiceen. Teil II.
Archiv für Protistenkunde 54 (2): 167-260. 3 pls. 1926.
- FARLOW, W. G. *The Synchytria of the United States.*
Botanical Gazette 10: 235-240. Pl. 4. 1885.
- TOBLER-WOLFF, GERTRUD. *Die Synchytrien. Studien zu einer Monographie
der Gattung.*
Archiv für Protistenkunde 28: 143-238. Pls. 10-13. 1913.
- COUCH, JOHN N. *Rhizophidium, Phlyctochytrium and Phlyctidium in the United
States.*
Journal of the Elisha Mitchell Scientific Society 47 (2): 245-260. Pls.
14-17. 1932.
- ATKINSON, GEO. F. *Some fungus parasites of algae.*
Botanical Gazette 48: 321-328. Figs. 1-8. 1909.

V. MONOBLEPHARIDALES (INCLUDING BLASTOCLADIALES), SAPROLEGNIALES (INCLUDING ANCYLISTIDACEAE)

- FITZPATRICK, HARRY M. *The lower fungi.* See above under Chytridiales.
- KANOUSE, BESSIE B. *A monographic study of special groups of water molds.*
I. *Blastocladiaceae.*
American Journal of Botany 14 (6): 287-306. Pls. 32-34. 1927.
- II. *Leptomitaceae and Pythiomorphaceae.*
Ibid. 14 (7): 335-357. Pl. 48. 1927.
- SPARROW, F. K. *The Monoblepharidales.*
Annals of Botany 47 (187): 517-542. Pl. 20 and Figs. 1-2. 1933.
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XI. "DISCOMYCETES," INCLUDING PEZIZALES, "HELVELLALES," PHACIDIALES, ETC. (EXCLUDING LICHENS)

In addition to the following see also various works in Part I and, under the Hymenomycetes and Agaricaceae several such as Ramsbottom, Velenovsky, Bigeard et Guillemin, Michael, etc.

- BOUDIER, ÉMILE. *Histoire et classification des Discomycètes d'Europe*. vii + 223 pp. Librairie des Sciences Naturelles. Paul Klincksieck. Paris. 1907.
- . *Icones mycologicae ou iconographie des champignons de France, principalement Discomycètes*. 4 vols. 600 colored plates. Paul Klincksieck. Paris. 1905-1910.
- SEEVER, FRED JAY. *The North American Cup-fungi. (Operculates)*. 284 pp. Frontispiece (colored) + 45 pls. 15 figures. Published by author. New York. 1928.
- NANNFELDT, J. A. *Studien über die Morphologie und Systematik der nichtlichenisierten inoperculaten Discomyceten*.
Nova Acta Regiae Societatis Scientiarum Upsaliensis Ser. IV. 8 (2): 1-368. Pls. 1-19. Figs. 1-47. 1932.
- DURAND, E. J. *The classification of the fleshy Pezizineae with reference to the structural characters illustrating the bases of their division into families*.
Bulletin of the Torrey Botanical Club 27 (9): 463-495. Pls. 27-32. 1900.
- This is a good discussion of the classification of these forms and gives a key to the genera and the families.
- SEEVER, F. J. *The Discomycetes of Eastern Iowa*.
Bulletin from the Laboratories of Natural History of the State University of Iowa 5: 230-297. Pls. 1-25. 1904.
- . *Discomycetes of North Dakota*.
Mycologia 1 (3): 104-114. 1909.
- Contains a key to the orders and genera of Discomycetes and notes on the occurrence of each species.
- BACHMANN, FREDA M. *Discomycetes in the vicinity of Oxford, Ohio*.
Proceedings of the Ohio State Academy of Science 5: 19-70. 1908.
- KILLERMAN, SEB. *Bayerische Becherpilze. I. Eupezizaceen. Mit kritischen Bemerkungen*.
Kryptogamische Forschungen der Bayerischen Botanischen Gesellschaft zur Erforschung der Heimischen Flora 2 (1): 27-47. 3 pls. 1929.
- RICK, J. *Monographia Pezizinearum Riograndensium*.
Brotéria. Revista de Ciencias Naturales. Série Botanica. 25 (2): 77-98. 1931, continued in Brotéria. Série Trimestral: Ciencias Naturais. 1 (1): 35-46, (2): 89-96, (3): 97-105. 1932.
- SEEVER, FRED J. *A Preliminary Study of the Genus Lamprospora*.
Mycologia 6 (1): 5-24. Pl. 114. 1914.
- . *North American Species of Aleuria and Aleurina*.
Ibid. 6 (6): 273-278. Pls. 142-144. 1914.
- . *North American Species of Ascodesmis*.
Ibid. 8 (1): 1-4. Pl. 172. 1916.
- . *The earth inhabiting species of Ascobolus*.
Ibid. 8 (2): 93-97. Pl. 184. 1916.
- . *Photographs and descriptions of cup fungi. IX. North American species of Discina*.
Ibid. 13 (2): 67-71. Pl. 4. 1921.

Includes key and descriptions of all recognized species of *Discina* in North America.

SEEVER, FRED J. *Photographs and descriptions of cup fungi. XIV. A new genus.*

Ibid. 23 (4): 247-251. *Pls.* 23-24. 1931.

The genus *Chloroscypha* with key and descriptions of the 4 known species.

———. *Photographs and descriptions of cup-fungi—XXI. The genus Calycina.*

Ibid. 26 (4): 344-347. *Pl.* 40. 1934.

KLIKA, JAROMIR. *Poznámky k výskytu druhů r. Humaria v Československu.*

[The species of *Humaria* in Czechoslovakia.]

Vestník Královské České Společnosti Nauk 1926 (12): 29 pp. 1927.

———. *O družicích r. Barlaea v Československu.*

Preslia 1926 (4): 14-19. 1 fig. 1926.

Diagnosis of 10 species of *Barlaea* (Pezizales) and sketches of 6.

KUPFER, ELSIE N. *Studies on Urnula and Geopyxis.*

Bulletin of the Torrey Botanical Club 29 (3): 137-144. 1902.

WHETZEL, H. H. *North American species of Sclerotinia.*

I. *Mycologia* 18 (5): 224-235. *Pls.* 27-29. *Fig.* 1. 1926.

II. *Ibid.* 21 (1): 5-32. *Pls.* 1-5. *Fig.* 1. 1929.

HONEY, EDWIN E. *The monilioid species of Sclerotinia.*

Mycologia 20 (3): 127-157. *Pls.* 17-19. *Figs.* 1-4. 1928.

ROUPPERT, C. *Révision du genre Sphacrosoma.*

Bulletin de l'Académie des Sciences, Cracovie, Classe Sci., Math., Nat.

1909: 75-95. 1909.

KILLERMANN, S. *Die Bulgaria—Fr.—Gruppe.*

Hedwigia 69 (1-2): 84-93. 1 pl. 1929.

A revision of the genera *Coryne*, *Bulgaria*, *Burkardia*, *Bulgariopsis* and *Neobulgaria*.

BOEDIJN, K. B. *The genus Sarcosoma in Netherlands India.*

Bulletin du Jardin Botanique de Buitenzorg Série III. 12 (2): 273-279.

Illustrated. 1932.

———. *The genera Phillipsia and Cookeina in Netherlands India.*

Ibid. 13 (1): 57-76. *Illustrated.* 1933.

HONE, DAISY S. *Minnesota Helvellineae.*

Minnesota Botanical Studies 3: 309-321. *Pls.* 48-52. 1904.

KILLERMANN, S. *Morcheln und andere Helvellaceen aus Bayern.*

Kryptogamische Forschungen der Bayerischen Botanischen Gesellschaft 3: 148-154. 1 fig. 1918.

RICK, J. *Monographia Helvellinearum Riograndensium.*

Broteria. Revista de Ciencias Naturales Série Botanica 25 (2): 72-76. 1931.

ANDERSON, P. J. and MARGUERITE G. ICKIS. *Massachusetts species of Helvella.*

Mycologia 13 (4-5): 201-229. *Pls.* 11-12. 1921.

Keys and descriptions of all species of *Helvella* in the Northeastern United States.

BOUDIER, E. *Révision analytique des morilles de France.*

Bulletin de la Société Mycologique de France 13: 129-153. 1897.

GRELET, L. J. *Les Discomycètes de France. Partie I. (Généralités; genres Morchella et Mitrophora).*

Bulletin de la Société Botanique du Centre-Ouest. 1932.

IMAI, SANSHI. *Contributions to the knowledge of the classification of the Helvellaceae.*

Botanical Magazine (Tokyo) 46 (544): 172-175. 1932.

Distinguishes five genera, *Helvellella* and *Neogyromitra* being described as new, listing all Japanese species (18), three described as new.

MASSEE, GEORGE. *A monograph of the Geoglossaceae.*

Annals of Botany 11 (42): 225-306. Pls. 12-13. 1897.

DURAND, E. J. *The Geoglossaceae of North America.*

Annales Mycologici 6 (5): 387-477. Pls. 5-22. 1908.

A very valuable work with full descriptions of all species and illustrations of many of them.

———. *New or noteworthy Geoglossaceae.*

Mycologia 13 (3): 184-187. 1921.

Supplementary to the preceding.

SINDEN, J. W. and H. M. FITZPATRICK. *A new Trichoglossum.*

Mycologia 22 (2): 55-61. Pl. 13. 1930.

A new species and corrections to Durand's paper.

LLOYD, C. G. *The Geoglossaceae.*

Mycological Writings 5. (Separate pagination) 1-24. Figs. 782-807. 1916.

Based largely on Durand's paper but with some modification of generic names and limits.

DURAND, ELIAS J. *The genus Catinella.*

Bulletin of the Torrey Botanical Club 49 (1): 15-21. 1922.

LUIJK, A. VAN. *Fungi van Nederland. I. Geoglossaceae van Nederland.*

Nederlandsch Kruidkundig Archief 1918: 111-144. 12 figs. 1919.

PALM, B. T. *On Cyttaria Berk. and Cyttariella n. gen.*

Annales Mycologici 30 (5-6): 405-420. Figs. 1-3. 1932.

A morphological and taxonomic study of the known species of *Cyttaria* and of *Cyttariella* an imperfect stage of the genus.

HAHN, GLENN GARDNER and THEODORE T. AYERS. *Dasyscyphae on conifers in North America: I. The large-spored white excipled species.*

Mycologia 26 (1): 73-101. Pls. 8-13. 1934.

II. *D. Ellisiana.*

Ibid. 26 (2): 167-180. Pls. 21-23. 1934.

VON HÖHNEL, FR. *System der Phacidiales v. H.*

Berichte der Deutschen Botanischen Gesellschaft 35: 416-422. 1917.

Gives a discussion and keys to families and genera of this group believed by the author to be intermediate between Pezizales and Dothideales.

See also Massee, British Fungus Flora, Vol. 4, for Discomycetes. (Above, under I. General Works.)

XII. TUBERALES

BATAILLE, F. *Flore analytique et descriptive des Tubéroïdées de l'Europe et de l'Afrique du Nord.*

- Bulletin de la Société Mycologique de France 37: 155-207. 1921.
 Tuberales and Elaphomycetaceae (and *Endogone*).
 HARKNESS, H. W. *California hypogaeous fungi*.
 Proceedings of the California Academy of Science, 3d Series 1: 241-292.
 Pls. 42-45. 1899.
 GILKEY, HELEN M. *A revision of the Tuberales of California*.
 University of California Publications in Botany 6: 275-356. Pls.
 26-30. 1916.
 ———. *Two new truffles*.
 Mycologia 12 (2): 99-101. Fig. 1. 1920.
 To be consulted in connection with the same author's foregoing paper.
 MURRILL, WM. A. *Another new truffle*.
 Mycologia 12 (3): 157-158. Fig. 1. 1920.
 See the foregoing reference.
 HESSE, R. *Die Hypogäen Deutschlands. Natur, und Entwicklungsgeschichte
 sowie Anatomie und Morphologie der in Deutschland vorkommenden Trüffeln
 und der diesen verwandten Organismen nebst praktischen Anleitungen bezüglich
 deren Gewinnung und Verwendung*. 2: 1-140. Pls. 1-II. Ludw.
 Hofstetter, Halle a. S. 1894. Tuberales.
 (Vol. 1. contains the Hymenogastrales.)
 BUCHOLTZ, F. *Beiträge zur Morphologie und Systematik der Hypogäen nebst
 Beschreibung aller bis jetzt in Russland angetroffenen Arten*. 196 pp.
 5 pls. Text figures. 1902. (Russian with German summary.)
 JACZEWSKI, ARTHUR LOUIS. *Monographie des Tuberacées de la Suisse*.
 Bulletin de l'Herbier Boissier 4: 591-602. 1896.
 FRIES, TH. M. *Skandinaviens tryfflar och tryffelliknande svampar*.
 Svensk Botanisk Tidskrift 3: 224-300. 1909.
 MASSEE, GEORGE. *The structure and affinities of the British Tuberaceae*.
 Annals of Botany 23 (90): 243-263. Pl. 17. 1909.
 See also, in Part I, Corda, Juillard-Hartmann, etc., and, under the Hymen-
 omyceteae, Bigeard et Guillemin, Velenovský, Ramsbottom, etc.

XIII. TAPHRINALES (EXOASCALES)

- SADEBECK, R. *Die parasitischen Exoasceen. Eine Monographie*.
 Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 10 (2):
 1-110. Pls. 1-3. 1893.
 GIESENHAGEN, KARL. *Taphrina, Exoascus und Magnusiella*.
 Botanische Zeitung 59, Erste Abtheilung. (7): 115-142. Pl. 5. 1901.
 PATTERSON, FLORA W. *A study of the North American parasitic Exoasceae*.
 Bulletin of the Laboratory of Natural History of the University of
 Iowa 3: 89-135. Pls. 1-4. 1895.
 ATKINSON, G. F. *Leaf curl and plum pockets*.
 Cornell University Experiment Station Bulletin 73: 319-355. Pls.
 1-20. 1894.
 PALM, BJ. *Svensk Taphrina-Arter*.
 Arkiv för Botanik 15 (4): 1-41. Figs. 1-9. 1918.
 A study of the Taphrinaceae of Scandinavia with keys to all the species.

JACZEWSKI, A. A. *Exoasci of Caucasus* (Russian).

Izvestiya S. Peterburgskovo Botanicheskovo Sada 1: 5-18. 1901.

XIV. HYSTERIALES

VON HÖHNEL, FRANZ. *Mycologische Fragmente. CCLXXII. Über die Hysteriaceen.*

Annales Mycologici 16 (1-2): 145-154. 1918.

Gives a key to the recognized genera of this family.

BISBY, G. R. *The literature on the classification of the Hysteriales.*

Transactions of the British Mycological Society 8: 176-189. 1923.

XV. SPHAERIALES

Many of the families and genera included in this list should probably be segregated under the Myriangiales, Hemisphaeriales and other groups which have been erected the last two or three decades.

ELLIS, J. B. and B. M. EVERHART. *The North American Pyrenomycetes.* iii + 793 pp. *Pls.* 1-41. Ellis and Everhart. Newfield, N. J. 1892.

This work contains not only Sphaeriales but also Erysiphales, Dothideales, Hypocreales and genera now removed to other orders as well.

BERLESE, A. N. *Icones fungorum omnium hucusque cognitorum ad usum Sylloges Saccardianae accommodatae.* Published by the author. Padua.

1: xiv + 243 pp. *Pls.* 1-162. *Generic plates* 1-22. 1894.

Lophiostomaceae and Sphaeriaceae; Phaeo- and Hyalophragmiae.

2: 1-216 pp. *Pls.* 1-178. *Generic plates* 1-10. 1900.

Sphaeriaceae; Phaeodictyae, Hyalodictyae, Scolecosporeae.

3: 1-120 pp. *Pls.* 1-172. 1905. Sphaeriaceae; Allantosporae.

TULASNE, L. R. et C. *Selecta Fungorum Carpologia.* See VIII, Ascomyceteae, Miscellaneous.

CHENANTAIS, J. S. *Études sur les Pyrénomycètes.*

Bulletin de la Société Mycologique de France 34: 47-73, 123-136,

Figs. 1-7. 1918. 35: 46-98, 113-139, *Pls.* 1-6, *Figs.* 8-25. 1919.

Takes up many of the fundamental bases for our present classification of this group and shows the errors. Discusses in particular the genera *Nitschkea*, *Lophiotrema*, *Rosellinia*, *Outhia*, *Massarinula*, *Lasiosordaria*, *Podospora* and various species of other genera.

SEAYER, FRED J. *Fimetariales.*

North American Flora 3: 57-88. 1910.

Includes Families Chaetomiaceae and Fimetariaceae (Sordariaceae).

CHIVERS, A. H. *A monograph of the genera Chaetomium and Ascotricha.*

Memoirs of the Torrey Botanical Club 14: 155-240. *Pls.* 6-17. 1915.

GRIFFITH, DAVID. *The North American Sordariaceae.*

Memoirs of the Torrey Botanical Club 11: 1-134. *Pls.* 1-19. *Figs.* 1-6. 1901.

STRATTON, ROBERT. *The Ascomycetes of Ohio. III. The Fimetariales of Ohio.*

Ohio Biological Survey 3: 75-144. *Pls.* 1-18. 1921.

SEEVER, FRED J. *The genus Lasiosphaeria.*

Mycologia 4 (3): 115-124. Pls. 66-67. 1912.

WELCH, DONALD S. *A monographic study of the genus Cucurbitaria in North America.*

Mycologia 18 (2): 51-86. Pls. 7-8. Figs. 1-5. 1926.

FITZPATRICK, HARRY M. *Monograph of the Coryneliaceae.*

Mycologia 12: 206-237, 239-267. Pls. 12-18. 1930.

———. *Monograph of the Nitschkieae.*

Ibid. 15: 23-44, 45-67. Pls. 1-7. 1923.

———. *The genus Fracchiaca.*

Ibid. 16 (3): 101-114. Pl. 10. 1924.

SHEAR, C. L., N. E. STEVENS and R. J. TILLER. *Endothia parasitica and related species.*

United States Department of Agriculture Bulletin 380: 1-82. Pls. 1-23. Figs. 1-5. 1917.

On pages 13-22 are given descriptions of the known species of Endothia.

VON HÖHNEL, FRANZ. *Mycologische Fragmente.*

CCIL. *Über die Diaporthe-Arten auf Aesculus.*

CCL. *Über die Diaporthe-Arten auf Caprifoliaceen.*

CCLI. *Über die Diaporthe-Arten auf Cornus.*

CCLII. *Über die Diaporthe-Arten auf Corylus.*

CCLIII. *Über die Diaporthe-Arten auf Eichen.*

CCLIV. *Über die Diaporthe-Arten auf Weiden.*

Annales Mycologici 16 (1-2): 116-122. 1918.

CCLXII. *Über die allantoidsporigen Sphaeriaceen.*

Ibid. 16 (1-2): 127-132. 1918.

An attempt to bring together in a more natural arrangement the Sphaeriales with allantoid spores. Gives a key to the genera thus brought together.

JACZEWSKI, ARTHUR LOUIS. *Monographie des Cucurbitariées de la Suisse.*

Bulletin de la Société Vaudoise des Sciences Naturelles, Lausanne 31: 67. 1895.

———. *Les Chaetomiées de la Suisse.*

Bulletin de l'Herbier Boissier 3: 494. 1895.

———. *Monographie des Calosphaeriées de la Suisse.*

Ibid. 4: 78-86. 1896.

———. *Étude monographique de la Famille des Sphaeriacees (Fuckel Jacz.) de la Suisse.*

Bulletin de la Société Mycologique de France 12: 86-119. Pl. 8. 1896.

RICK, J. *Monografia das Valsineas do Rio Grande do Sul.*

Broteria. Serie Trimestral. Ciencias Naturais. 2 (2): 83-99. 1933.

———. *Monographia Sphaerialium astromaticorum Riograndensium.*

Ibid. 2 (3): 133-145, (4): 169-201. 1933.

WEHMEYER, LEWIS E. *The genus Diaporthe Nitschke and its segregates.*

University of Michigan Studies. Scientific series 9: i-x, 1-349. Pls.

1-18. University of Michigan Press. 1933.

———. *The British species of the genus Diaporthe Nits. and its segregates.*

Transactions of the British Mycological Society 17 (4): 237-295. 1933.

- CHENANTAIS, J. E. *Notice taxonomique sur le groupe Melanomma*.
Bulletin de la Société Mycologique de France 38: 88-92. 1922.
- . *Études sur les Pyrenomycetes. VII. Les Lasiosordariées*.
Ibid. 35: 68-86. Pl. 1. Figs. 12-15. 1919.
- RAMSEY, GLEN B. *The genus Rosclinia in Indiana*.
Proceedings of the Indiana Academy of Science 1914: 3-16. Pls. 1-3. 1914.
- RICK, J. *Monografia das Rosclinias Riograndenses*.
Brotéria. Série Trimestral. Ciencias Naturais 1: 183-192. 1932.
- JACZEWSKI, ARTHUR LOUIS. *Monographie des Massariées de la Suisse*.
Bulletin de l'Herbier Boissier 2: 661. 1894.
- . *Les Xylariées de la Suisse*.
Bulletin de la Société Mycologique de France 11: 108-137. Pl. 12. 1895.
- ELLIS, J. B. and B. M. EVERHART. *Synopsis of the North American species of Xylaria and Poronia*.
Journal of Mycology 3 (9): 97-102, (10): 109-113. 1887.
- . *Synopsis of the North American species of Hypoxylon and Nummularia*.
Ibid. 4 (4-5): 38-44, (7): 66-70, (9): 85-93, (11): 109-113. 1888.
5 (1): 19-23. 1889.
- LLOYD, C. G. *Synopsis of some genera of the larger Pyrenomycetes: Camillea, Thamnomycetes, Engleromyces*.
Mycological Writings 5: 1-16. Figs. 826-857. 1919.
- (Note: This section is paged separately from the remainder of this volume.)
- . *The larger Pyrenomycetes. Second paper*.
Ibid. 5: 1-16. Figs. 1444-1460. 1919. (This is also paged separately from the remainder of the volume.)
- . *Xylaria notes. No. 1*.
Ibid. 5: 1-16. Figs. 1200-1236. 1918.
- . *Xylaria notes. No. 2*.
Ibid. 5: 1-16. Figs. 1324-1357. 1918.
- (Both papers are paged separately, pages 1-16.)
- HAWKINS, STACY. *Some Xylarias of Indiana*.
Proceedings of the Indiana Academy of Science 35: 225-229. 1925.
- VAN DER BYL, P. A. *Die Swamfämilie Xylariaceae in die Unie van Suid-Afrika*.
Annale van die Universiteit van Stellenbosch 10A (3): 1-10. 1932.
- . *South African Xylarias occurring around Durban, Natal*.
Transactions of the Royal Society of South Africa 9 (2): 181-183. Pls. 7-8. 1921.
- CHILD, MARION. *The genus Daldinia*.
Annals of the Missouri Botanical Garden 19 (4): 429-496. Pls. 26-33. 1932.
- THEISSEN, FERDINAND. *Xylariaceae Austro-Brasilienenses I. Xylaria*.
Denkschrift der K. Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Klasse. 83: 47-86. 11 pls. 7 figs. 1927.

RICK, J. *Monographia das Hypoxyleas Riograndenses.*

Brotéria. Revista de Ciencias Naturaes. Série Botânica 25 (1): 21-50. 1931.

———. *Monographia Boliniarum Riograndensium.*

Ibid. 25 (2): 65-71. 1931.

Boliniaceae, near Xylariaceae. Also a key to the genera of Xylariaceae (including the above family).

XVI. HYPOCREALES

SEEVER, FRED. J. *Hypocreales.*

North American Flora 3: 1-56. 1910.

———. *The Hypocreales of North America.*

I. Mycologia 1 (2): 41-76. Pls. 4-5. 1909.

II. Ibid. 1 (5): 177-207. Pl. 13. 1909.

III. Ibid. 2 (2): 48-92. Pls. 20-21. 1910.

IV. Ibid. 3 (5): 207-230. Pls. 53-54. 1911.

ELLIS, J. B. and B. M. EVERHART. *Synopsis of the North American Hypocreaceae, with descriptions of the species.*

Journal of Mycology 2 (3): 28-31, (5): 49-51, (6): 61-69, (7): 73-80, (9): 97-99, (10): 109-111, (11): 121-125, (12): 133-137. 1886; 3 (1): 1-6. 1887.

WEESE, J. *Beiträge zur Kenntnis der Hypocreaceen.* I. Mitteilung.

Sitzungsberichte der K. Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse 125: 465-575. Pls. 1-3. Figs. 1-15. 1916.

IMAI, SANSHI. *Studies on the Hypocreaceae of Japan.* I. *Podostroma.*

Transactions of the Sapporo Natural History Society 12: 114-118. 2 figs. 1932.

5 species of *Podostroma* are listed with key for their identification.

PODZIMEK, JAN. *K monografi ceskych namehi.* (Claviceps.)

Časopis Narodního Musea. Část přírodovědná. 106: 16-35. 1932.

MASSEE, GEORGE. *A revision of the genus Cordyceps.*

Annals of Botany 9 (33): 1-44. Pls. 1-2. 1895.

LLOYD, C. G. *Synopsis of the Cordyceps of Australasia.*

Mycological Writings 4. Separate pagination 1-12. Figs. 611-626. 1915.

PETCH, T. *Studies in entomogenous fungi.* II. *The genera Hypocrella and Aschersonia.*

Annals of the Royal Botanical Garden of Peradeniya 7: 167-278. Pls. 2-7. 1921.

See also Ellis and Everhart under the Sphaeriales, above.

XVII. DOTHIDEALES

THEISSEN F. und H. SYDOW. *Die Dothideales.*

Annales Mycologici 13 (3-6): 149-746. Pls. 1-6. 1915.

A very fine monograph, including some families subsequently removed to some of the groups listed below.

- STEVENS, F. L. and NORA DALBY. *Some Phyllachoras from Porto Rico*.
Botanical Gazette 68 (1): 54-59. Pls. 6-8. 1919.
- JACZEWSKI, ARTHUR LOUIS. *Les Dothidéacées de la Suisse*.
Bulletin de la Société Mycologique de France 11: 155-195. Pl. 14.
1895.

XVIII. ERSYPHACEAE

- SALMON, ERNEST S. *A monograph of the Erysiphaceae*.
Memoirs of the Torrey Botanical Club 9: 1-292. Pls. 1-9. 1900.
- . *Supplementary notes on the Erysiphaceae*.
Bulletin of the Torrey Botanical Club 29 (1): 1-22, (2): 83-108, (4):
181-210, (5): 302-316, (11): 647-649. Pls. 9-11. 1902.
- BURRILL, T. J. and F. S. EARLE. *Parasitic Fungi of Illinois. Part II.*
Erysiphaceae.
Bulletin of the Illinois State Laboratory of Natural History 2: 387-432.
Figs. 1-8. 1887.
- KELSEY, F. D. *The genus Uncinula*.
Oberlin College Laboratory Bulletin 7: 1-15. 10 figs. 1897.
- O'KANE, W. C. *The Ohio Powdery Mildews*.
The Ohio Naturalist 10 (7): 166-176. Pls. 9-10. 1910.
- FINK, BRUCE. *Notes on the powdery mildews of Ohio*.
Ohio Journal of Science 21 (6): 211-216. Figs. 1-2. 1921.
- SALMON, E. S. *The Erysiphaceae of Japan*.
Bulletin of the Torrey Botanical Club 27 (8): 437-450. Pl. 1. 1900.
- JORSTAD, IVAR. *The Erysiphaceae of Norway*.
Norske Videnskaps-Akademi Matematisk-Naturvidenskabelig
Klasse. Skrifter 1925 (10): 1-116. 2 figs. 1926.
- Discusses distribution, hosts, etc., of the 25 species of the family in Norway.
- TAI, F. L. and C. T. WEI. *Notes on Chinese fungi. II. Erysiphaceae*.
Sinensia. Contributions of the Metropolitan Museum of Natural
History Nanking 3 (4): 93-130. *Illust.* 1932.
- SĂVULESCU, TR. and C. SĂNDU-VILLE. *Die Erysiphaceen Rumaniens*.
Annales Scientifiques de l'Académie des Hautes Études Agronomiques
de Bucarest 1: 1-82. 24 pls. 1929. Also published separately by
Tipografia "Bucovina" in Bucarest.
- POLLACI, G. *Monographia delle Erysiphaceae italiane*.
Atti del Reale Istituto Botanico dell'Università di Pavia. 2 ser. 9.
30 pp. 1 pl. 1905.
- JACZEWSKI, ARTHUR LOUIS. *Monographie des Erysiphées de la Suisse*.
Bulletin de l'Herbier Boissier 4: 721-755. 1896.
- BLUMER, S. *Die Formen der Erysiphe cichoracearum DC.*
Centralblatt für Bakteriologie Parasitenkunde und Infektionskrank-
heiten. Zweite Abteilung 57 (1-3): 45-60. 1922.
- . *Die Erysiphaceen Mitteleuropas mit besonderer Berücksichtigung der*
Schweiz.
Beiträge zur Kryptogamenflora der Schweiz 7 (1): 1-483. Figs. 1-167.
1933.

ARNAUD, G. *Étude sur les champignons parasites. (Parodiellinacées, inclus Erysiphacées) [Les Astérinées II].*

Annales des Épiphyties 7: 1-115. Pls. 1-10. Figs. 1-25. 1921.

The author unites in the family Parodiellinaceae the subfamilies Parodiellineae, Parodiopsidae and Erysipheae with keys to the genera and lists of the species.

MAURIZIO, ANNA MARIA. *Zur Biologie und Systematik der Pomaceen bewohnenden Podosphaeren. Mit Berücksichtigung der Frage der Empfänglichkeit der Pomaceenpropfbastarde für parasitische Pilze.*

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XIX. MELIOLACEAE (PERISPORIACEAE)

GAILLARD, ALBERT. *Contribution à l'étude des champignons inférieures.*

Famille des Périsporiacées. Le genre Meliola: anatomie, morphologie, systématique. Thèse. 164 pp. 24 pls. P. Klincksieck. Paris. 1892.

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Bulletin de la Société Mycologique de France 8: 176-188. Pls. 14-16. 1892.

STEVENS, F. L. *The genus Meliola in Porto Rico.*

Illinois Biological Monographs 2: 475-554. Pls. 1-5. 1916.

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Botanical Gazette 64 (5): 421-425. Pls. 24-26. 1917.

Illustrations of the type specimens of the species of *Meliola* described, mainly from Argentine, by Dr. Carlos Spegazzini.

———. *The Meliolinae.*

I. *Annales Mycologici* 25 (5-6): 405-469. Pls. 1-2. 1927.

II. *Ibid.* 26 (3-4): 165-383. Pls. 2-6. 1928.

STEVENS, F. L. and L. R. TEHON. *Species of Meliola and Irene from British Guiana and Trinidad.*

Mycologia 18 (1): 1-22. Pls. 1-2. 1926.

BEELI, M. *Note sur le genre Meliola.*

Bulletin du Jardin Botanique de l'État, Bruxelles 7 (1): 89-160. 1920.

Contains a key to all known species of *Meliola*.

———. *Notes mycologiques. I. Contribution à la flore mycologique du Congo.*

Ibid. 8 (1): 1-11. Pl. 1. 1922.

Descriptions of additional species of *Meliola* and of other fungi.

SPEGAZZINI, CARLOS. *Revisión de las Meliolas Argentinas.*

Anales do Museo Nacional de Historia Natural Buenos Aires 32: 339-393. 1924.

DOIDGE, E. M. and H. SYDOW. *The South African species of the Meliolinae.*

Bothalia 2 (2): 424-472. 1928.

DIPPENAAR, B. J. *'n Bydrae tot ons Kennis van die Suid-Afrikaanse Geslagte en Soorte van die Familie Polystomellaceae Theiss. en Syd.*

Annale van die Uniwersiteit van Stellenbosch 8A (2): 1-38. Figs. 1-3. 1930.

DOIDGE, ETHEL M. *South African Perisporiaceae*.

I. Transactions of the Royal Society of South Africa 5: 713-750. *Pls.* 55-66. 1917.

II. Revisional Notes. *Ibid.* 7: 193-197. 3 *figs.* 1919.

III. *Ibid.* 8: 107-143. 1920.

MARTIN, GEORGE. *Synopsis of the North American species of Asterina, Dimerosporium and Meliola*.

Journal of Mycology 1 (11): 133-139, (12): 145-148. 1885.

MENDOZA, JOSÉ MIGUEL. *The Philippine species of Parasterina*.

Philippine Journal of Science 49 (3): 443-459. 15 *pls.* 1932.

ARNAUD, GABRIEL. *Contribution à l'étude des Fumigines*.

Annales de l'École Nationale d'Agriculture de Montpellier. Nouvelle Série. 9: 239-277. *Pls.* 1-3. *Figs.* A-C. 1909; 10: 211-330. *Figs.* 1-29. 1910; 12: 23-54. *Figs.* 1-13. 1912.

The second and third parts have systematic studies of the sooty molds.

JACZEWSKI, ARTHUR LOUIS. *Les Capnodiètes de la Suisse*.

Bulletin de l'Herbier Boissier 3: 603-606. 1895.

XX. MICROTHYRIACEAE AND HEMISPHAERIACEAE

THEISSEN, F. and H. SYDOW. *Synoptische Tafeln*.

Annales Mycologici 15 (6): 389-491. *Figs.* 1-38. 1917.

This paper contains keys to the families and genera of the Orders Hemisphaeriales and Myriangiales, and also of the Order Perisporiales. It is the culmination of the work reported in part in the papers immediately below.

THEISSEN, F. *Hemisphaeriales*.

Annales Mycologici 11 (5): 468-469. 1913.

Contains keys to Family Hemisphaeriaceae.

———. *Lembosia-Studien*.

Ibid. 11 (5): 425-467. *Pl.* 20. 1913.

———. *Ueber Membranstrukturen bei den Microthyriaceen als Grundlage für den Ausbau der Hemisphaeriales*.

Mycologisches Centralblatt 3 (6): 273-286. *Pl.* 1. 1913.

Contains keys to the families of the order and to the genera of the families Microthyriaceae and Hemisphaeriaceae.

———. *Trichopeltaceae n. fam. Hemisphaerialium*.

Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten. Zweite Abteilung. 39 (23-25): 625-640. 1 *pl.* 7 *figs.* 1914.

———. *Zur Revision der Gattung Dimerosporium*.

Beihefte zum Botanischen Centralblatt. Zweite Abteilung. 29: 45-73. 1912.

Since the name *Dimerosporium* is unavailable the species for which this name has been used have been distributed among 6 or more genera. This paper gives a key to these genera and brief descriptions of the more available species.

———. *Die Gattung Asterina*.

Abhandlungen der K. K. Zoologisch-Botanischen Gesellschaft in Wien 7 (3): 1-130. *Pls.* 1-8. 1913.

Gives full descriptions of 119 species in the 3 sections *Euasterina*, *Dimersporium* and *Clypeolaster*. Gives a generic key distinguishing *Asterina* and the 10 other genera of Microthyriaceae with 2-celled ascospores.

THEISSEN, F. *Zur Revision der Gattungen Microthyrium und Seynesia*.

Oesterreichische Botanische Zeitschrift 62: 216-221, 275-280, 327-329, 395-396, 420-435. 1912; 63: 121-131. 1913.

DOIDGE, ETHEL M. *South African Microthyriaceae*.

Transactions of the Royal Society of South Africa 8: 235-282. Pls. 13-19. 1920.

RYAN, RUTH W. *The Microthyriaceae of Porto Rico*.

Mycologia 16 (4): 177-196. 1924.

Mostly consists of new species, some old species being listed but not described.

THEISSEN, F. *Die Trichothyriaceen*.

Beihefte zum Botanischen Centralblatt. Zweite Abteilung. 32 (1): 1-16. Pl. 1. Figs. 1-3. 1914.

VON HÖHNEL, FRANZ. *Ueber die Trichothyriaceen*.

Berichte der Deutschen Botanischen Gesellschaft 35: 411-416. 1917.

Discussion of structure of perithecium and relationship of the family, and of the composition of the Order Perisporiales.

———. *Fragmente zur Mykologie*. X. Mitteilung.

Sitzungsberichte der K. Akademie der Wissenschaften (Wien). Mathematisch-Naturwissenschaftliche Klasse 119: 393-473. 1910.

Contains a key to the didymosporous Microthyriaceae.

TEHON, L. R. and G. L. STOUT. *Notes on the parasitic fungi of Illinois*. IV.

Mycologia 21 (4): 180-196. Pl. 13. 1929.

Contains a key distinguishing 5 genera of Family Stigmatiaceae, Order Hemisphaeriales.

XXI. MISCELLANEOUS "PERISPORIALES," "PSEUDOSPHERIALES," MYRIANGIALES

COTTON, A. D. *The genus Atichia*.

Royal Botanical Gardens, Kew. Bulletin of Miscellaneous Information 1914: 54-63. Figs. 1-5. 1914.

Discusses the known species. Called by French writers *Seuratia*. Author believes it goes best in the Perisporiales as a special family Atichiaceae.

VON HÖHNEL, FRANZ. *Fragmente zur Mykologie*.

Attention may be called to the following papers under this title:

IV. Mitteilung.

Sitzungsberichte der K. Akademie der Wissenschaften (Wien) Mathematisch-Naturwissenschaftliche Klasse 116: 615-647. 1907.

Discussion of the family Pseudospheriaceae.

VI. Mitteilung.

Ibid. 118: 275-452. Pl. 1. Figs. 1-35. 1909.

Revision of Family Myriangiaceae and of the genus *Saccardia*, and of the Family Cookellaceae. Discussion of the relationship of these to the Pseudospheriaceae and Dothideaceae.

XI. Mitteilung.

Ibid. 119: 617-679. 1910.

Key to genera of Capnodiaceae and to those Dothideaceae with superficial ascus stroma.

THEISSEN, F. und H. SYDOW. *Die Gattung Parodiella*.

Annales Mycologici 15 (1-2): 125-142. 1917.

———. *Vorentwürfe zu den Pseudosphaeriales*.

16 (1-2): 1-34. Figs. 1-5. 1918.

THEISSEN, F. *Mykologische Abhandlungen*.

Verhandlungen der Zoologisch-Botanischen Gesellschaft, Wien. 66: 296-400. Pl. 1. 1916.

A discussion of the families Pseudosphaeriaceae and Englerulaceae and of the genus Physalospora.

———. *Studie über Botryosphaeria*.

Annales Mycologici 14 (5): 297-340. 1 fig. 1916.

PETCH, T. *Studies in entomogenous fungi. V. Myriangium*.

Transactions of the British Mycological Society 9: 45-80. Pls. 2-3.

Fig. 1. 1924.

In addition to the foregoing, the following series of papers includes keys to families and genera and also to species in some cases, in an arrangement not at all similar to the old classification but at least in part approximating the truth more closely.

ARNAUD, G. *Les Astérinées*.

Annales de l'École Nationale d'Agriculture de Montpellier. Nouvelle Série 16: 1-288. Pls. 1-53. Figs. 1-22. 3 maps. 1918.

———. [Les Astérinées II] *Étude sur les champignons parasites. (Parodiellinacées, inclus Erysiphées.)*

Annales des Épiphyties 7: 1-115. Pls. 1-10. Figs. 1-25. 1921.

———. [Les Astérinées III] *Étude sur les champignons parasites. (Parodiellinacées, suite.)*

Ibid. 9: 1-40. Pls. 1-10. 1923.

———. *Les Astérinées, IV partie. (Études sur la systématique des champignons pyrénomycètes.)*

Annales des Sciences Naturelles. Botanique. Xme série. 7: 643-723. Pls. 1-16. Figs. 1-25. 1925.

———. *Les Astérinées V. (Études sur les champignons parasites) Caliciacées, Hemisphériacées, etc.*

Annales des Épiphyties 16 (5): 235-302. Pls. 1-14. Figs. 1-15. 1930.

———. *Les Astérinées VI. Champignons astérinoïdes de l'Herbier du Muséum.*

Recueil de Travaux Cryptogamiques dédiés à Louis Mangin. 8 pp. Pls. 4-5. 3 figs. Paris. 1931.

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Annales de Cryptogamie Exotique 4: 74-97. Pls. 2-7. 1931.

XXII. ASPERGILLALES (PLECTASCALES)

DODGE, CARROLL W. *The higher Plectascales.*

Annales Mycologici 27 (3-4): 145-184. *Pls.* 1-2. *Figs.* 1-2. 1929.

Description of all the species of *Trichocomaceae* and *Elaphomycetaceae*.

See also Bataille, under *Tuberales*, above, and the various authors referred to upon *Aspergillus* and *Penicillium*, under the *Fungi Imperfecti* below.

XXII. SACCHAROMYCETALES (FOR TORULA, TORULOPSIS, ETC., SEE ALSO FUNGI IMPERFECTI)

KOHL, FRIEDRICH GEORG. *Die Hefepilze, ihre Organisation, Physiologie, Biologie und Systematik, sowie ihre Bedeutung als Gärungsorganismen.* viii + 343 pp. *Pls.* 1-8. Quelle und Meyer. Leipzig. 1908.

GUILLIERMOND, ALEXANDRE. *Les levures.* xii + 565 pp. 163 figs. O. Doin et fils. Paris. 1912.

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Bulletin Trimestriel de la Société Mycologique de France 43: 245-258. *Pl.* 10. *Figs.* 1-6. 1927.

BUSCHKE, A. und A. JOSEPH. *Die Sprosspilze.* [In: KOLLE, W. und A. VON WASSERMANN. *Handbuch der pathogenen Mikroorganismen* 3. Auflage. Band 5, Teil 1, Lieferung 14.] Pp. 321-400. 1 col. pl. 32 figs. Gustav Fischer. Jena. 1928.

STELLING-DEKKER, N. M. *Die Hefesammlung des "Centraalbureau voor Schimmelcultures."* Beiträge zu einer Monographie der Hefesorten. Erster Teil. *Die sporogenen Hefen.*

Verhandelingen der Koninklijke Akademie van Wetenschappen te Amsterdam. Afdeling Natuurkunde (Tweede Sectie). Deel 28. No. 1. vii + 547 pp. *Illustrated.* 1931.

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XXIV. USTILAGINALES

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 North American Flora 7 (1): 1-82. 1906.
- . *The Ustilaginaceae, or smuts, of Connecticut*.
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 5: 1-45. Figs. 1-55. 1905.
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 Transactions and Proceedings of the New Zealand Institute 55: 397-433.
 7 pls. 1924.
- . *Third supplement to the New Zealand Uredinales and Ustilaginaceae*.
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- . *Fourth supplement to the Uredinales and Ustilaginales of New Zealand*.
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- . *Fifth supplement to the Uredinales and Ustilaginales of New Zealand*.
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- . *Seventh supplement to the Uredinales and Ustilaginales of New Zealand*.
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- MCALPINE, D. *The smuts of Australia*. vii + 288 pp. Pls. 1-56. Figs.
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- SCHELLENBERG, H. C. *Die Brandpilze der Schweiz*.
 Beiträge zur Kryptogamenflora der Schweiz 3 (2): i-xlvi, 1-180.
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 1 (2): 77-97. 1924.
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Annales Mycologici 20 (3-4): 228-237. Figs. 1-4. 1922.

Distinguishes all the recognized species of the genus.

See also Plowright, below under Uredinales.

XXV. UREDINALES

SYDOW, P. et H. *Monographia Uredinearum seu specierum omnium ad hunc usque diem descriptio et adumbratio systematica.* Gebrüder Borntraeger. Leipzig.

1: i-xxxv, 1-972. 45 pls. 1904. The genus *Puccinia*.

2: i-xix, 1-396. 14 pls. 1910. The genus *Uromyces*.

3: 1-728. 32 pls. 1915. The remainder of the Pucciniaceae and families Melampsoraceae, Zaghouaniaceae and Coleosporiaceae.

4: i-iv, 1-670. 1924. Uredineae Imperfecti (*Peridermium*, *Accidium*, *Monosporidium*, *Roestelia*, *Cacoma*, *Uredo*, *Maïpea*).

KLEBAHN, H. *Die wirtswechselnden Rostpilze.* xxxvii + 447 pp. Pls. 1-6. Gebrüder Borntraeger. Berlin. 1904.

HARTOT, PAUL. *Les Uredinées (Rouilles des plantes).* xv + 392 pp. 47 figs. Octave Doin. Paris. 1908.

This is the first volume issued of the Bibliothèque de Botanique Cryptogamique directed by L. MANGIN, one of the series of Toulouse, Encyclopédie Scientifique.

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ARTHUR, JOSEPH CHARLES. *Uredinales.* (F. D. KERN, F. D. FROMME, H. S. JACKSON, E. B. MAINS, C. R. ORTON, collaborating.)

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Ibid. 55: 1-58. 1924.

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Annales Mycologici 31 (1-2): 1-40. 1933.

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1: i-lxxi, 1-416. Figs. 1-208. 1924.

2: i-viii, 1-421. Figs. 1-174. 1925.

The first volume contains the genus *Puccinia* alone, the second volume the other genera of rusts.

HOLWAY, E. W. D. *North American Uredineae.*

Parts I-V, Pls. 1-54. 1905-1924.

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Contributions from the Arnold Arboretum of Harvard University 2: 1-138. Pls. 1-9. 1932.
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INDEX

A

- Abe, Seiji, 24
Abies, 267, 273
Absidia, 109
 glauca, 106, 108
Acer, 164
 rubrum, 164
Acervulus, 376
Achlya, 67, 68, 69, 70, 71, 85, 96
 americana, 70
Achlyogeton, 75
 Acrasiales, 28, 29, 35
Acrasis, 30
 Acrogenous conidial chains, 126
Actinomyces, 383
 bovis, 383
 scabies, 383
Actinonema, 162
 Adaptations, 5
 Aecial chain, 260
 primordium, 259, 260, 262, 263
Aecidium, 276, 374
 Aeciospore, 254, 259, 260
 Aecium, forms of, 271
 Agaricaceae, 9, 201, 325, 340, 341,
 342, 343, 344, 349, 351, 358,
 362, 391
 differential characters, 349
 discharge of spores, 349
 Agaricales, 296, 310, 317, 318, 323,
 343, 372
 asexual reproduction, 325
Agaricum, 12
 Fungus, 10
Agaricus, 11, 13, 345, 350, 353, 358
 arvensis, 128, 344, 353
 campestris, 128, 308, 344, 345, 353
 rodmani, 346
 Albuginaceae, 83, 89, 91
Albugo, 8, 89, 90, 91, 92, 96, 102
 bliti, 90, 91
 candida, 89, 92
 ipomoeae-panduranae, 91
 portulacae, 90, 91, 94
 tragopogonis, 91
 Alder, 173
Aleurodiscus, 326
Alina, 225
 Alismataceae, 285
 Allantosphaeriaceae, 197, 198
 Allen, Ruth F., 17, 109, 257, 259, 261,
 262, 263, 264, 269
Allomyces, 4, 8, 57, 58, 59, 61, 63, 68, 78
 arbuscula, 62
 javanicus, 61
Alnus, 173
Alternaria, 126, 194, 387
 brassicae, 387
 var. *nigrescens*, 387
 solani, 387
 violae, 387
 Alternation of generations, 8
Althaea rosea, 268
Amanita, 11, 105, 347, 352, 358
 caesarea, 10, 345
 muscaria, 347
 phalloides, 347
 rubescens, 345
Amaranthus, 91
Amauroderma, 338
Amaurosporae, 349
Ambrosia, 50
Amerosporae, 377
 Ames, L. M., 17, 132, 183, 184, 185,
 187, 188, 244, 264, 302
 Ammiaceae, 120
Amoeba, 23

- Amorphomyces salagriae*, 142
 Amphigynous antherids, 87
Amphisphaeria, 192
 Amphisphaeriaceae, 192
Amygdalus persica, 173, 382
Anaptychia ciliaris, 149
Ancylistes, 76
 Ancylistidaceae, 35, 59, 66, 67, 75, 77, 120
 Ancylistidales, 59
Andropogon sorghum, 282
 Andrus, C. F., 17, 261, 262, 264
 Angiocarpic apothecium, 155
 Angiospermae, 82
Annularia, 350
 Annulus, 349
 Antherid, 135, 136, 137, 139, 141, 184
Anthoceros, 284
 Anthophyta, 82, 219, 254, 275
Anthostoma, 197, 198
Anthurus borealis, 370
Aphanomyces, 67, 69, 72
 exoparasiticus, 67
Aplanes, 70, 119
 Aplanospore, 101, 119
 Apothecium, 132, 133
 size and shape, 133, 154
 Apple, 194, 195, 267, 345, 379
Araiospora, 75
 pulchra, 74
Archangeliella, 360
 Archicarp, 142, 144
Arcyria, 27
Armillaria, 352
 mellea, 3, 9, 344, 345, 391
 Arnaud, G., 206, 219, 220, 225, 227
 Arnold, Chester, A., 185
 Aronescu, Alice, 188
 Arthur, J. C., 252, 268, 273, 275
Aschersonia, 379
Asclepias, 50
Ascobolus, 152, 154, 156, 157
 carbonarius, 152, 153, 156
 immersus, 157
 magnificus, 157
 stercorarius, 155, 156
Ascochyta, 378
 pisi, 194, 378
 Ascocorticiaceae, 171, 172, 173, 310
Ascocorticium, 172, 318
 Ascogenous hyphae, 124, 137, 150, 308, 309
 Ascogonium, 135, 139, 148, 149, 150, 152, 153, 163, 184
 Ascohymeniales, 135
Ascoidea, 239, 243, 244
 rubescens, 241
 Ascoideaceae, 236, 237, 239
 Ascoideae, 238
 Ascoloculares, 135, 192, 195
 Ascomyceteae, 3, 8, 119, 125, 127, 129, 130, 132, 179, 218, 235, 236, 240, 243, 244, 245, 246, 247, 286, 301, 308, 316, 317, 358, 374
 Ascomycetes, 251
Ascophanus, 157
 granuliformis, 155
Ascoscleroderma, 234
 Ascospore, 129
 development, 138
 discharge, 133, 155, 181
 form, 181
 Ascus, 8, 129, 251
 development, 132
 Asexual reproduction, 9
 Ashby, S. F., 242
 Ashworth, Dorothy, 270
 Asparagus, 268
Asparagus officinalis, 268
 Aspergillaceae, 126, 230, 231, 245
 Aspergillales, 152, 213, 218, 219, 228, 229, 245, 246
 sexual reproduction, 229
Aspergillus, 12, 110, 229, 231, 383, 384
 herbariorum, 233
 niger, 384
Aster, 275
 Asteraceae, 92, 120, 284
Asterina, 207
 camelliae, 208
Astraeus, 369
Astrothelium, 199

Atanasoff, D., 133
 Atkinson, George F., 77, 140, 235, 244,
 314, 332, 350
Auricularia, 11, 13, 297, 312
 auricula-judae, 298
 sambucina, 298
 Auriculariaceae, 312
 Auriculariales, 129, 285, 286, 297, 310,
 315, 316, 317, 318
 Autoecious rusts, 266, 267
Avena sativa, 267, 282
 Avocado, 195
 Azygospore, 100, 118

B

Bachmann, Freda M., 149, 150, 153
Bacidea rubella, 146
 Backus, Myron P., 163
 Bacteria, 1
 dissociation, 238
 Balanced parasitism, 125
 Banker, H. J., 331
 Baranetzky, J., 234
 Barberry, 261, 262, 266, 267, 268
 Barley, 267, 278, 282
 Barrage sexual, 305
 Barrett, J. T., 37
 Bartlett, A. W., 47
 de Bary, Anton, 1, 16, 17, 22, 77, 88,
 92, 221, 233, 235, 266
 Basidia, 8
 development of, 295
 different types of, 296
 tuning-fork type, 297, 317
 two-spored, 295, 302, 324
Basidiobolus, 115, 116
 ranarum, 115, 116
 Basidiomycetae, 3, 125, 127, 129, 130,
 141, 251, 252, 254, 263, 285,
 286, 294, 298, 306, 307, 374,
 391
 genetics of sexuality, 303, 305
 sexual phases, 302
 sexual reproduction, 300
 Basidiomycetes, 251

Basidiophora, 92
 entospora, 94
 Basidiospore, 129, 130, 252
 discharge, 298
 Basidium, 129, 252
 Basigenous conidial chains, 126
Battarea, 369
 Bauch, Robert, 17, 280, 281, 282, 304,
 306
 Bauhin, Gaspard, 10
 Baur, F., 149
 Baxter, Dow V., 336, 345
 Bean, 268, 325, 391
 Beech, 241
 Beet, 378
 Beetles, 144
 Bell morel, 159
 Bender, Harold B., 374, 376, 379, 380,
 382
 Bennett, Alfred W., 251
 Bensaude, Mathilde, 17, 302, 306, 307
Berberis vulgaris, 261, 266, 267
 Berlese, A. N., 90, 94, 220
 Bessey, Charles E., 127, 129, 251
 Ernst A., 140
Beta vulgaris, 378, 388, 391
 Betts, E. M., 156
Betula, 340
 Biological races, 254
 Bipolar sexuality, 304, 305
 Birch, 340
 Bird's-nest fungi, 363
Bjerkandera, 336
 Black Raspberry, 267
 Blackberry, 267
 Blackman, V. H., 200, 260, 264
 Blain, W. L., 204
Blakeslea, 104, 105, 106, 111
 trispota, 112
 Blakeslee, A. F., 17, 105
Blastocladia, 63
 globosa, 63
 pringsheimii, 62
 Blastocladiaceae, 59, 60, 61
 Blastocladales, 59
 Blodgett, H. T., 353
 Blue-green Algae, 146

- Blumer, S., 224
 Boedijn, K. B., 310, 312
 Boletaceae, 341, 351
 Boletellus, 351
 meruloides, 342, 351
 Boletus, 11, 12, 13, 296, 342
 edulis, 7, 341
 luteus, 342
 satanas, 341
 Boss, Georg, 280
 Botryodiplodia, 378
 Botrytis, 12, 161, 384
 cinerea, 385
 convoluta, 385
 Boudier, Émile, 157
 Bovista, 11, 366
 plumbea, 367
 Brand Fungi, 251
 Brassica, 387
 Brassicaceae, 91, 95
 Braxton, H. H., 70, 72
 Bread yeast, 238, 239
 Brefeld, Oscar, 16, 101, 106, 161, 233,
 235, 251, 278, 283, 285, 298,
 308, 313, 314, 316, 333
 Bremia, 91, 95
 lactucae, 94, 95
 Brevilegnia diclina, 68
 Brodie, H. J., 5, 299, 300, 301, 305
 Bromus, 203, 224
 Broomeia, 368
 Brown, A. M., 262
 H. B., 187
 W. H., 139
 Brunswik, H., 305, 308
 Bryophyta, 284
 Bryopsis, 78
 Bucholtz, Fedor, 114, 167
 Budding yeasts, 237, 238
 Buisman, Christine, 190, 191
 Buller, A. H. R., 110, 128, 263, 299,
 301, 307, 340, 343
 Bunt, 278, 284
 von Büren, Günther, 119, 120
 Burgeff, H., 106
 Burk, Myrie, 34
 Burkholder, W. H., 211, 212
 Burt, E. A., 325
 Butler, E. J., 47, 86
 C
 Cabbage, 387
 Cadman, Elsie J., 24
 Cacoma, 276, 374
 Calcium carbonate, 3
 Callose, 3, 58
 Calocera, 317
 Calvatia, 365, 366
 maxima, 127, 366
 Calyptospora, 273
 goeppertiana, 272
 Canavalia, 211
 Cane blight of Rubus, 378
 Cantharellus, 351, 352
 cibarius, 345
 Capillitium, 25, 30, 35, 357
 Capnodiaceae, 218, 219, 227
 asexual reproduction, 227
 sexual reproduction, 227
 Capnodium, 218, 219
 citri, 227
 salicinum, 227, 228
 Carex, 282
 Carleton, Mark A., 254
 Carnation, 267, 389
 Carpomycetaceae, 124, 129
 Carposporic branches, 144
 Cassell, R. C., 283
 Castanea dentata, 198
 Catastoma, 367
 circumscissum, 367
 Catenaria, 47
 Cauliflower, 387
 Cayley, Dorothy M., 24
 Celery, 379
 Cellulin, 61, 73
 Cellulose, 3, 25, 30, 38, 39, 47, 58, 59,
 60, 66, 73, 78, 100, 120, 125,
 144, 244, 245
 Celtis, 95
 occidentalis, 219
 Cephalosporium, 190, 383, 389

- Cephalothecium*, 385
 roseum, 385
Ceracea, 317
Ceratiomyxa, 26, 27
 fruticulosa, 26
Ceratostomataceae, 190
Ceratostomella, 189, 190
 adiposa, 187
 coerulea, 187
 fimbriata, 184, 185
 paradoxa, 191
 piceae, 187
 pilifera, 190
 pini, 190
 pluriannulata, 187
 ulmi, 5, 190, 191, 389
Cercosphaerella, 184, 194
Cercospora, 387
 beticola, 388
 cerasella, 194, 388
 rha pontici, 387
Ceratomyces crassus, 7, 341
Cetraria islandica, 152
Ceuthospora, 378
Chaetochloa, 92
Chaetocladiaceae, 111
Chaetocladium, 104, 111
Chaetomiaceae, 189
Chaetomium, 185, 189
Chamaesyce, 257
Cherry, 194, 345, 388
Chestnut, American, 198
Chiaetobasidial nuclear division, 295,
 297, 314
Chitin, 3, 33, 39, 47, 58, 59, 60, 100,
 118, 125, 144, 244, 245
Chlamydospore, 9, 69, 120, 127, 252
Chloriodide of zinc, 60, 66, 73, 78, 120
Chlorochytrium, 52, 77
Chlorococcum, 77, 146
Chlorophyceae, 2, 145, 146
Chlorosplenium aeruginosum, 128, 161
Choanephora, 104, 111
 conjuncta, 112
Choanephoraceae, 111
Christensen, J. J., 277
Christman, A. H., 264, 270
Chroococcus, 146
Chrysomyxa, 274
Chrysotrix nolitangere, 125
Chytridiales, 7, 35, 57, 65, 66, 77, 120,
 129
Cichoriaceae, 120
Circinella minor, 101
Cirrus, 378
Citromyces, 232
Citrus, 195, 228
Cladochytriaceae, 35, 44, 46, 65, 66,
 77, 119
Cladochytrium, 47
 replicatum, 47
Cladonia, 147
 rangiferina, 146
Cladosporium, 126, 386
 cucumerinum, 386
 herbarum, 386
Clamp connections, 127, 254, 281, 294,
 306, 307, 308, 309, 310, 313,
 316, 323, 327, 333, 334, 344,
 356, 360, 374, 391
 in Ascomyceteae, 168, 307
 in Smuts, 277
Clathraceae, 370
Clathrales, 371
Clathrus, 11, 12, 371
 cancellatus, 370
Claudopus, 350
Claussen, P., 136, 137, 139
Claustula, 370
Clavaria, 11, 12, 13, 317, 329, 330
 pistillaris, 329
 subbotrytis, 330
Clavariaceae, 328, 391
Claviceps, 9, 202
 purpurea, 200, 202
Clavicipitaceae, 201, 202
Clemencet, Marion, 234
Clinton, G. P., 47, 88, 93
Clitocybe, 352
 illudens, 347
 infundibuliformis, 345
Clover, 386
Club-root, 33
Clusius, C., 10

- Clypeus, 192
 Cobb, N. A., 5
Coccomyces, 162, 163, 382
Codium, 78
 Coenocyte, 83
 Coker, W. C., 70, 72, 329, 330, 331, 364, 365, 369, 371
 Coleoptera, 144
Coleosporium, 256, 271, 272, 275
 solidaginis, 275
Collema, 144, 145, 148, 150, 151, 184
 cheileum, 146
 crispum, 149
 nigrescens, 146
 pulposum, 150
Collemodes, 148, 150, 153
 bachmannianum, 149
Colletotrichum, 195, 380
 gloeosporioides, 380, 389
 malvarum, 381
 Colley, R. H., 255, 264
Collybia radicata, 345
 velutipes, 345
Coltrichia, 337
 Columella, 27, 103, 104, 357, 362
Completoia, 117
 Compositae, 91, 92, 120, 284
 Conidia, 82, 104, 105, 111, 112, 113, 115, 125, 126
 Conidial distribution, 126
Conidiobolus, 116
 Conifers, 254, 257
 Coniomycetes, 129
Coniothyrium, 378
 fuekelii, 378
 Conjugate division, 137, 252, 306
 Conjugation tube, 67, 68, 71, 84, 86, 90
 Convergence in evolution, 22
 Cook, W. R. Ivimey, 31, 34, 38
 Cooper, D. C., 86
Coprinus, 5, 305, 308, 325, 348, 350, 353
 atramentarius, 343, 345
 comatus, 345, 346, 353
 ephemerus, 302
 ephemerus var. *bisporus*, 302
 Coprinus fimetarius, 304
 lagopus, 300, 301, 304, 307
 micaceus, 353
 sterquilinus, 307, 343
Copromyxa, 30
Corallofungus, 11
Coralloides, 11, 12
 Corda, A. C. J., 14
Cordyceps, 202
 Coremium, 126
Coriollus, 338
Coriolopsis, 337
Coriolus, 337
 Corn smut, 278
 Corner, E. J. H., 134, 155
Corticium, 318, 324, 325, 326, 327, 328, 331, 341, 358
 pratensis, 324
 vagum, 325, 326, 391
 Cortina, 349
Cortinari, 347, 352
Coryneum, 381
 beijerinckii, 381
 Cotner, Frank B., 60, 64
 Cotton, 239, 242, 390, 392
 Couch, John N., 42, 43, 67, 68, 72, 112, 311
 Craigie, J. H., 17, 261, 264
 Cranberry, 328
Craterellus, 326, 351
Crepidotus, 350
Cronartium, 266, 272, 274
 cerebrum, 274
 ribicola, 255, 257, 267, 268
Crucibulum, 363
 Crucifers, 91, 95
Cryptosporus, 338
 volvatus, 338
Ctenomyces, 234
 Cucumber, 93, 386
Cucumis melo, 95, 387
 sativus, 95, 386
Cucurbitaria, 192
 Cucurbitariaceae, 191, 205
Cudonia, 166
 Cunningham, G. H., 361, 370
Cunninghamella, 104, 111

Currant, 267
 Curtis, K. M., 40, 41
Cyathus, 363
 schweinitzii, 363
 stercoreus, 364
 striatus, 363

Cydonia, 194
Cylindrosporium, 163, 382
Cyphella, 326
Cystidia, 323, 328
Cystobasidium, 310
Cystopsora, 272
Cystopus, 89
Cystosorus, 38
 Cytogamy, 139
Cytospora, 197, 378
Cytaria, 155, 166
 gunnii, 166
 Cyttariaceae, 166

D

Dacryomitra, 317
Dacryomyces, 298, 299, 317
 chrysocomus, 316
 deliquescens, 316
 lutescens, 316
 Dacryomycetaceae, 317
 Dacryomycetales, 297, 310, 316, 317,
 318, 319
 Dade, H. A., 191
Daedalea, 340, 341, 351
 confragosa, 340
Daldinia, 198
 concentrica, 198
 Dale, Elizabeth, 233, 234
 Dangeard, P. A., 16, 137, 139, 141, 184,
 222, 223, 230, 233, 234, 235,
 244, 295, 299, 309, 316
 Daniels, E., 387
 Darwin, Charles, 157
Dasyscypha, 161
Dasyscypha foveolata, 271
 Dematiaceae, 382, 386
Derbesia, 78
 Dermateaceae, 162
 Destructive parasitism, 125

Deuteromyceteae, 130
 Dewberry, 267
 Dianthaceae, 279, 282
Dianthus caryophyllinus, 267, 389
 Diaporthaceae, 197, 200, 244
Diaportha, 197, 381
 Diatoms, 2
 Diatrypaceae, 195
Diatrype, 197, 198
Diatrypella, 197
 Dicaryon, 8, 129, 137
 phase, 323
 stage, 252, 253, 254
Dichotomosiphon, 78
 Dickinson, Sydney, 280, 281, 282
 Dicotyledoneae, 275
Dicranophora, 104, 108, 111
Dictydium, 27
 cancellatum, 28
Dictyophora duplicata, 370, 371
 Dictyosporae, 377
Dictyostelium, 30
 mucroides, 29
Dictyuchus, 70, 72
 achyloides, 70
 polysporus, 72
Didymella, 211
 iridis, 387
Didymium, 24, 27
 difforme, 24
 squamulosum, 25
 Didymosporae, 377
 Dietel, P., 251, 268, 273, 275, 283
 Dillenius, J. J., 11, 13
 Diplanetic zoospores, 69
Diplocarpon, 162
 soraueri, 380
Diplodia, 378
 Diploidization, 263, 301, 302
Dipodascus, 239, 241, 243, 244, 245
 albus, 240
 Diptera, 144
Discella, 380
Disciseda, 367
 Discomyceteae, 206
 Discomycetes, 132, 145
Discula, 195, 380

- Disjunctor, 89, 261
 Disk Lichens, 145
 Disk of stroma, 196
 Dissociation of yeasts, 237
Doassansia, 279, 285
Doassansiopsis, 285
 marthianoffiana, 283
 Dodge, B. O., 17, 140, 152, 153, 187,
 188, 257, 264, 270, 281, 295,
 313
 C. W., 234, 235, 359, 360, 372
 Dothideaceae, 203, 204
 Dothideales, 203, 204, 205, 208, 219
 Dothioraceae, 209, 210
 Dowding, E. S., 187
 Drayton, F. L., 17, 140, 152, 156, 264,
 385
 Drechsler, Charles, 5, 49, 210
Drepanopeziza ribis, 162
 Duggar, B. M., 379, 385
 Durand, E. J., 157, 165, 166
 Durum wheat, 254
 Dutch elm disease, 190, 388
- E
- Earth star, 368
Echinodontium, 331
 Ectostroma, 196
 Edgerton, C. W., 187
 Edible mushrooms, 345
 Edson, H. A., 83, 86
 Effused stroma, 196
 Eftimiu, Panca, 296, 328
 Eidam, E., 116, 234
Elaphomyces, 234
 Elaphomycetaceae, 231, 234
Elfringia, 338, 339
 megaloma, 340
 Elliott, J. A., 184, 185, 186, 387
 Ellis, J. B. and B. M. Everhart, 191,
 221, 225
Elsinoe, 211
 canavaliae, 211
 phaseoli, 211
 pyri, 211
 veneta, 211, 212
Elvela, 13, 159
 infula, 159
 Elvelaceae, 158, 165
 Elvelales, 165
Elymus, 203
Empusa, 117
Endocarpion miniatum, 146
 Endogonaceae, 113
Endogone, 108, 113
 fasciculata, 113
 lactiflua, 114
 malleola, 114
Endomyces, 236, 243, 244, 245
 capsulatus, 237
 magnusii, 236
 Endomycetaceae, 236, 238, 241
Endophyllum, 269, 270
 euphorbiae-sylvaticae, 269, 270
 sempervivi, 269
Endoptychum, 362
 Endospore, 133
 Endosporeae, 25, 27
Endothia, 198
 parasitica, 198
 Englerulaceae, 219, 227
Entoloma, 347
Entomophthora, 116, 117, 118
 fresenii, 116
 grylli, 118
 muscae, 115, 118
 sepulchralis, 116
 Entomophthorales, 59, 100, 114, 118,
 124, 125, 247
Entomosporium, 162
 maculatum, 380
Entophlyctis, 44
 Entostroma, 196
Entyloma, 277, 284
Eocronartium, 310
 musciicola, 285
 Epibasidium, 297, 317, 318, 319, 327
Epichloe, 202
Epicoccum, 390
 Epiplasm, 132
 Episporium, 132
 Epithecium, 207
 Eremascaceae, 238

Eremascus, 236
 Ericaceae, 274
 Eriksson, J., 254
Eriaceus, 12, 13
 Ergot, 200, 202
 Erysiphaceae, 126, 218, 219, 224, 227,
 229, 230
 asexual reproduction, 220
 biological races, 224
 sexual reproduction, 221
 Erysiphales, 218, 228, 229, 230, 245,
 246
Erysiphe, 218, 223, 224
 cichoracearum, 224
 graminis, 220, 224, 254
 Eubasidiaceae, 296, 310
 Eumyceteae, 129
Euphorbia, 257
Eutypella, 197
 linearis, 191
Excipula, 380
 Excipulaceae, 380
 Excipulum, 134
Exidia, 315
 glandulosa, 313
 Exoascales, 170, 309
Exoascus, 140, 173
 Exobasidiaceae, 327, 328
Exobasidium, 323, 324, 325
 rhododendri, 296, 328
 vaccinii, 327, 328
 Exosporeae, 24, 26, 27
Exosporium, 390

F

Fabian, F. W., 237
Fagus, 241
 Fairchild, D. G., 116
 Falck, R., 133, 156, 335
 Farlow, W. G., 346
 Fawcett, G. L., 380
Femisia, 317
 Fenner, E. Aline, 112
 Ferns, 254, 267, 273, 310
 Filamentous Fungi, 57
Fimetaria, 185, 189
 fimicola, 187
 Fimetariaceae, 189
 Finger-and-toes, 33
 Fir, 267, 273
 Fischer, Eduard, 167, 230, 231, 360,
 369, 372
 Fission yeasts, 237, 238
Fistulina, 12, 342
 hepatica, 343
 Fistulinaceae, 342
 Fitzpatrick, H. M., 1, 36, 59, 77, 82,
 88, 117, 119, 244, 285
 Randal E., 171, 172
 Flagellata, 2
 Flagellum number, 60
 Flax, 389
 Flerov, B. K., 276, 281, 295
 Flor, H. H., 284
 Florideae, 2, 127, 134, 140, 141, 149,
 151, 179, 246, 247
 Flowering Plants, 219, 254, 275
 Fly-speck fungus, 379
Fomes, 10, 12, 336, 338, 341
 annosus, 333
 applanatus, 128, 332, 340
 fomentarius, 339
 igniarius, 332, 339
 laricis, 128, 332, 339
 officinalis, 339
 pinicola, 339
 ungulatus, 339
Fomitella, 338
 Form genus, 375
 Forsberg, J. L., 262
 Fox-tail grasses, 92
Fragaria, 193
 Fraser, Helen C. I., 153
 Freeman, E. M., 254
 Frey, C. N., 184, 194
 Fries, Elias Magnus, 13, 129, 251
Fuligo, 24, 27
 septica, 28
 Fungi, definition of, 2
 distribution by insects, 5
 Fungi Imperfecti, 130, 163, 170, 182,
 328, 374, 375

Fungi lamellati, 12
Fungi porosi, 12
Fungi pulverentes, 12
Fungi ramosi, 12
Fungoides, 11.
Fungus, 10, 11, 12, 351
Funiculi, 363
Fusarium, 201, 383, 389
 graminearum, 390
 lini, 389
 oxysporum, 389
 sesami, 6, 128
 vasinfectum, 390
Fusicladium dendriticum, 194
Fusicoccum, 195

G

Galløe, Olaf, 146
Gallowaya, 256
Gametangia, 58
Gametophyte, 62
Ganoderma, 338, 339
 curtisii, 339
 isugae, 339
Gasteromyceteae, 296, 310, 356, 369,
 372
 origin of, 358
 structure of spore-fruit, 357
Gastromyceteae, 356
Gäumann, Ernst A., 1, 95, 111, 140,
 204, 205, 209, 213, 235, 244,
 252, 296, 312, 358, 372
Gäumann-Dodge, 334
Gautieria, 358
 graveolens, 357
 plumbea, 359
Geaster, 12, 365, 367, 369
 hygrometricus, 369
 rufescens, 365
Geastraceae, 372
Geitler, Lothar, 145
Gemmae, 300
Genea, 167, 168
Genistellaceae, 118
Geoglossaceae, 165

Geoglossum, 134, 165, 166
 glabrum, 165
Geographic races, 282, 305
Geolegnia, 70, 119
Giant puffball, 127
Gibberella, 201
 saubinetii, 201, 390
Gilbert, E. N., 310
 Frank A., 23
Gills, 343
Gleba, 357
Globifomes, 338
Gloeoglossum, 166
Glocosporium, 195, 212, 375, 380, 381,
 382
 ribis, 162, 381
 venetum, 211, 212
Glomerella, 195, 375
 cingulata, 187, 195, 380
Gnomonia, 195, 375
 veneta, 195
Gnomoniaceae, 195, 375, 381
Gobi, C. J., 50
Gonapodya, 61, 78
 prolifera, 61
Gooseberry, 219, 267
Goplana, 272
Gossypium, 239, 242, 390, 392
Graff, Paul W., 226
Grape, 193, 219
Graphis elegans, 146
Graphium, 388
 ulmi, 190, 388
Grasses, 284
Green, Ethel, 156
Green Algae, 146
Gregory, C. T., 92
Grifolia, 336
Griggs, Robert F., 51
Grossularia, 219, 267, 268
Grove, W. B., 268
Guepinia, 316
Guignardia, 193, 378
 bidwellii, 193
Guilliermond, A., 237, 238, 239, 242,
 243
von Gutenberg, H. L., 39

- Guthulina*, 30
Guthulinopsis clavata, 29
 Gwynne-Vaughan, Helen C. I., 137, 139, 218
Gymnoascaceae, 231, 234, 245
Gymnoascus reessii, 234, 235
Gymnocarpic apothecium, 155
Gymnoconia, 276
 interstitialis, 257, 262, 267, 270
Gymnosporangium, 12, 13, 261, 269, 276
 juniperi-virginianae, 267, 268
 sabinae, 266
Gyrocephalus, 315
- H
- Hackberry, 95, 219
 Hadley, Philip, 238
 Hanna, W. F., 17, 262, 277, 281, 282, 305
 Hansen, E. C., 239
Haplographium, 386
Haploravenelia, 276
Haplosporella, 378
Harpellaceae, 118
 Harper, R. A., 16, 136, 137, 139, 221, 222, 223, 251, 295, 309
Harpochytrium, 43
 Hartig, Robert, 272
 Harvey, James V., 71
Harveyella mirabilis, 2
 Hasselbring, H., 388
 Hatch, Winslow, R., 62
Haustoria, 4, 58, 91, 251, 254, 255, 265, 277, 323
Hebeloma, 347
 Hedgcock, G. G., 190
 Hein, Illo, 222, 223
Helianthus, 261
 annuus, 267, 268
Helicobasidium, 310
 filicinum, 310
Helicosporae, 377
Helminthosporium, 386
 terres, 211, 386
Helotiaceae, 161
Helotiales, 159, 160
Helotium, 66, 161
Helvella, 159
Helvellaceae, 158
Hemiascus, 245
Hemibasidii, 251
Hemigaster, 358
Hemisphaeriaceae, 207
Hemisphaeriales, 204, 205, 206, 213, 219, 228, 379
 sexual reproduction, 206
 Hemlock, 339
 Hemp, 95
 Herbarium mold, 231
Hericum, 331
 caput-ursi, 330
 coralloides, 330, 331
Heterobasidiaceae, 297, 310
Heteroecious Rusts, 266, 267
Heteroecism, proof of, 266
Heterosporium, 386
 gracile, 386
Heterolextus, 316
 alpinus, 316
Heterothallic Agaricaceae, 344
 Saprolegniaceae, 66, 72
Heterothallism, 105, 107, 156, 302, 303, 334
Hicoria, 328
 Higgins, B. B., 163, 184
Higginsia, 162, 382
 Higher Fungi, 3, 119, 124
 Hirmer, Max, 308
 History of mycology, 10
 von Höhnelt, F., 135, 182, 205, 206
Holcus sorghum, 282
 Hollyhock, 268
Holobasidium, 319
 Homma, Yasu, 224
Homobasidiaceae, 296, 310
Homothallic Agaricaceae, 344
 Mucorales, 105, 107
 Saprolegniaceae, 66, 72
Homothallism, 302, 303
 Honey dew, 227
 Hopkins, E. W., 59, 100, 125

- Hops, 95
Hordeum sativum, 282
 Horn, L., 57
 Howard, Frank L., 24
Humaria, 157
 granulata, 139
Humarina, 157
 Hüttig, Werner, 279, 280
 Hyalodictyae, 377
 Hyalodidymae, 377, 378, 380, 381, 385
 Hyalophragmiae, 377, 380, 381, 385,
 389
Hyaloria, 315
 Hyaloriaceae, 315
Hyalospora, 273
 Hyalosporae, 377, 378, 379, 380, 383,
 388, 389
 Hydnaceae, 329, 330, 341, 392
 Hydnangiaceae, 362
Hydnangium, 362
Hydnotria, 167
Hydnum, 13, 314, 315, 331, 392
Hydrophora, 109
Hygrophorus, 345
 Hymenial cavities, 357
 Hymenium, 133, 294, 323, 356
Hymenochaete, 326
Hymenogaster, 362
 Hymenogastraceae, 362
 Hymenogastrales, 358, 370, 371, 372
 Hymenogastrineae, 372
 Hymenomyceteae, 323
 Hymenoptera, 144
 Hyphal bodies, 115, 117
 Hyphochytriaceae, 44, 59, 64, 65
Hyphochytrium, 66
Hypholoma, 352
 appendiculatum, 345, 353
 candolleianum, 305
 sublateritium, 353
 Hyphomyceteae, 382
 Hypobasidium, 297, 312, 317, 318, 319,
 327
Hypochnus, 324, 326
Hypocopra, 185, 189
Hypocrea, 201
 Hypocreaceae, 201
 Hypocreales, 134, 180, 189, 199, 202,
 203, 213, 219, 229, 379, 390
 sexual reproduction, 200
 Hypodermataceae, 170
 Hypodermeae, 251
 Hypodermii, 129
Hypomyces, 201
 Hypostroma, 207
 Hypothecium, 134, 207
Hypoxyton, 187, 198, 201
 marginatum, 191
 Hysterangiaceae, 362
 Hysteriaceae, 170
 Hysteriales, 145, 169, 170, 192, 207
Hysterium insidens, 169
Hysterographium fraxini, 170
 minutum, 169
Ilystrix, 203
- I
- Identification of fungi, 393
 Imperfect Fungi, 182, 374, 389
 Incompatibility, 188, 303
 Indian corn, 92
 Inner veil, 349
Inocybe, 347
Inoderma, 337
Inonotus, 336
 Inoperculatae, 154
 Infertility, 188
 Internal promycelium, 256
 Introduction, 1
Ipomoea batatas, 91, 102
Irene, 227
Iris, 387
Irpex, 330, 331
Isaria, 388
Isoachlya, 69
 Isolated stroma, 196
- J
- Jackson, H. S., 254, 268
 Jaczewski, Arthur L., 50
 Jahn, E., 1
 Jenkins, Anna E., 211

- Jola*, 310, 311, 312
lasioboli, 310
 Jolivette, Hally D. M., 109, 110
 Jones, Fred Reuel, 49
 Philip M., 34
 S. G., 153, 164
 Juel, H. O., 171, 240, 295, 296, 318
Juglans, 328
Juniperus, 276
 virginiana, 267, 268

K

- Kanouse, Bessie B., 7
 Karling, John S., 45, 47
 Karyogamy, 129, 139
 Keene, Mary Lucile, 107
 Kharbush, S., 140, 296, 328
 Killermann, S., 308, 334
 Killian, Karl (Charles), 184, 186, 194,
 200, 206
 Klebahn, Heinrich, 86, 184, 194, 375,
 381
 Klebs, Georg, 7
 Kniep, Hans, 17, 59, 62, 280, 282, 302,
 307
 Kny, L., 150
 Kotila, J. E., 324
Kunkelia nitens, 257, 262, 269, 270,
 281, 295
 Kusano, S., 40

L

- Laboulbeniales, 125, 127, 132, 133, 139,
 141, 151, 179, 180, 246
 Labyrinthulales, 28, 30, 35
Lachnea scutellata, 158
 stercorea, 153
Lactarius, 105, 348
 deliciosus, 345
 volemus, 345
Lactuca sativa, 381
Laetiporus, 336
 speciosus, 336
Lagenidium, 76
 rabenhorstii, 76

- Lagerheim, G. de, 240, 314
 Lamellae, 343
 Larch, 275, 339
Larix, 161, 275, 339
Lasiobotrys, 225
 Latex, 348
Lecanora lentigera, 146
 Lecanorales, 132, 139, 141, 145, 152,
 153, 159, 161, 180, 182, 246
 Leger, L., 118
 Lehfeldt, W., 263, 301
Lembosia, 207
 Lendner, A., 101, 106, 107
Lentinus, 351, 352
Lenzites, 340, 341, 351
 betulinus, 340
Leotia, 166
 chlorocephala, 165
Lepiota, 105, 350, 352
 morgani, 347
 naucina, 345
 procera, 345, 352
Leptolegnia, 69
 caudata, 68
 Leptomitaceae, 59, 60, 67, 72, 78, 82,
 83, 96
 Leptomitales, 59
Leptomitus, 73
 lacteus, 70, 73
Leptosphaeria, 195, 205, 209, 211
 coniothyrium, 378
Leptostroma, 380
 Leptostromataceae, 163, 379
Leptothyrium pomi, 379
 Lettuce, 381
Leucogaster, 361
 Leucosporae, 349
Leucostoma, 197, 198
Leveillula, 219, 220, 223
 taurica, 220
 Levine, M., 296
 Levisohn, Ida, 115
 Lichen, 13, 126, 145, 146, 147, 246
 asexual reproduction, 148
 sexual reproduction, 148
Ligniera, 34
 Lima bean, 211

- Limacinia*, 228
 Lindau, G., 166, 195, 218, 219, 374
 Lindegren, C. C., 17
 Lindfors, T., 269
 Linnaeus, Carolus, 11, 12
 Linne, Carl von, 12
Linum usitatissimum, 389
 Lister, Arthur, 23, 28
 Literature cited, 18, 52, 78, 96, 121,
 130, 173, 213, 247, 286, 319,
 353, 372, 392
 Literature for identification of fungi,
 393
 Litmus, 6, 128, 152
 Lloyd, C. G., 370
 Lohman, M. L., 169, 170
 Lohweg, H., 172
 Long-cycle rusts, 268
 Loose smut, 278
Lophiostoma, 192
 Lophiostomataceae, 170, 192
Lophium mytilinum, 169
Lophodermium, 163
 Lorenz, Franz, 357
 Lower fungi, 124
 Lumpy jaw, 383
 Lupo, Patsy, 187
Lychnis, 279
 Lycoperdaceae, 365, 372
 Lycoperdales, 358, 365, 369
 Lycoperdineae, 372
Lycoperdon, 11, 12, 13, 366
 gemmatum, 367
Lycopersicum, 239, 379
- M
- Macrochytrium*, 65
 Macrocytic rusts, 268
Macrophoma, 377, 378
Macrosporium, 387
Magnusiella, 173
 Mains, E. B., 254
 Maire, René, 296, 309
 Maize, 92, 267, 282, 390
 smut, 278, 279
 Malaceae, 276
Malus, 194, 195
 malus, 267
 Malvaceae, 268
Mangifera, 195
 indica, 380
 Mangin, L., 59, 100
 Mango, 195, 380
Marasmius, 344
 caryophylleus, 345
 oreades, 345
Marssonina, 162
 panattoniana, 381
 Martens, P., 300
 Martin, G. W., 316, 318
 Massee, Geo., 264
Massospora, 115, 118
 Matthews, Velma D., 84
 Mattiolo, O., 168, 307
 McCullough, N. B., 237
Medicago sativa, 162
 Meiosis, 8, 27
 Meiotic division (see also meiosis,
 reduction division), 26, 27
Melampsora, 272, 275, 286
 lini, 264
 Melampsoraceae, 273, 275
 Melanconiaceae, 380
 Melanconiales, 376, 380
 Melanconidaceae, 195
 Melanin, 128
Melanogaster, 361
Melanospora, 199
 Melanosporaceae, 189
 Melanosporae, 349
 Melhus, I. E., 89, 92
Meliola, 205, 218, 219, 227, 228
 bidentata, 225
 circinans, 226
 Meliolaceae, 218, 219, 224, 227
 asexual reproduction, 225
 sexual reproduction, 225
 Melogrammataceae, 195
Merulius, 333, 334
 domesticus, 335
 lacrymans, 332, 335
Mesophellia, 234
 Metaphyses, 205

- Meyer, J., 384
 Mez, Carl, 2, 78, 247, 285, 358
 Micheli, P. A., 12, 13, 351
 classification of fungi, 12, 351
 Microconidia, 156
 Microcyclic rusts, 269
Microglossum, 165
Micromyces, 42
 zygogonii, 42
Micropeltis, 208
Microsphaera, 223
 quercina, 225
Microstroma juglandis, 328
 Microthyriaceae, 205, 206, 207, 219,
 228
Microthyrium, 207
 Milbrath, D. G., 94
 Milburn, Thomas, 129
Milesina, 273
 Miller, Julian, 134, 180, 182, 191, 212,
 213, 231
 Miller, L. W., 331
 von Minden, M., 59
Mitula, 165
 Mittmann, Gertrud, 185, 186, 187
 Möller, A., 298
Mollisia, 162
 Mollisiaceae, 162, 375, 380, 381, 382
Monadelphus, 347
 Monascous cavities, 205
 hymenia, 207, 208
Monascus, 230, 232
 sexual reproduction, 232
Monilia, 152, 161
 Moniliaceae, 382, 383, 392
 Moniliales, 170, 376, 382
Monilinia, 161
 Monoblepharidaceae, 63
 Monoblepharidales, 39, 50, 52, 57, 58,
 59, 60, 64, 77, 78, 119
Monoblepharis, 8, 59, 63, 66, 68, 78
 fasciculata, 64
 macrantha var. *laevis*, 64
 polymorpha, 63, 64
 Monocaryon stage, 252, 253, 254, 323
 Monoplanetic zoospores, 69
 Montemartini, L., 389
 Moore, Morris, 237
 M. B., 283
Morchella, 11, 12, 13, 134, 159, 317
 conica, 160
 Moreau, Fernand, 141, 151, 269, 307
 Mme. F., 264
 Morel, 159
Mortierella, 103, 108, 113
 rostafinskii, 101, 106
 Mortierellaceae, 112, 114
 Mosses, 285, 310
 Mounce, Irene, 17, 302
Mucor, 12, 13, 102, 104, 106, 108, 109,
 111, 244
 hiemalis, 106
 mucedo, 106, 107, 108
 rouxii, 100
 Mucoraceae, 109
 Mucorales, 8, 58, 59, 100, 102, 103,
 105, 108, 110, 115, 118, 119,
 124, 125, 127, 156, 243, 244,
 247
Mucronoporus, 337
 Murphy, P. A., 87, 88
 Murray, George, 251
 Murrill, W. A., 334, 338, 341, 342
Musca domestica, 118
Muscus saxatilis vel lichen, 10
 Mushroom, development of, 348
 tests for edibility, 348
 Muskmelon, 95, 387
Mulinus caninus, 370
Mycenastrum, 367
Mycelia Sterilia, 376, 391
 Mycetozoa, 1, 23, 29, 35, 36, 129
 Mycology, definition, 1
Mycosphaerella, 184, 193, 378, 379, 386
 cerasella, 194, 388
 fragariae, 193
 pinodes, 194, 378
 sentina, 193
 tabifica, 194
 Mycosphaerellaceae, 193, 206
Mycotypha, 112
 Myriangiaceae, 231
 Myriangiales, 204, 205, 211, 213

- Myriangium*, 231
 bambusae, 212
 duriaei, 211, 212
Myxamoebae, 24
Myxomyceteae, 23
Myxophyceae, 145, 146
Myxosporium, 380, 381
Myzocytiium, 76
- N
- Nannfeldt, J. A., 134, 135, 140, 157,
 159, 160, 162, 170, 189, 192,
 195, 204, 205, 213, 382
Nectria, 201
 cinnabarina, 201, 389
Nectriaceae, 201
Nectrioidaceae, 379
Nematospora, 239
 coryli, 239
 gossypii, 239
 Nero, 10
 Net blotch of barley, 211
 Net plasmodium, 30
 Neuhoﬀ, W., 285, 318
Neurospora, 18, 188, 189, 264
 sitophila, 188
 tetrasperma, 187
 Newton, Margaret, 262
 Dorothy E., 302, 304
 Nicholson, W. H., 38
Nidularia, 363
Nidulariaceae, 363, 364
Nidulariales, 358, 363, 364
Nidulariineae, 372
 Nienburg, W., 200
Nigroporus, 338
Nitschia, 2
 Non-filamentous fungi, 22
 Non-motile sperms, 179, 184, 246
 Non-saccharomycetaceae, 239
Nostoc, 13, 145, 146, 148
Nothofagus, 155, 166
Nowakowskiella, 47
 Nowell, W., 242
 Nurse cells, 223
Nyctalis, 344
- O
- Oak, 336, 339
 Oat, 267, 281, 282
 smut, 278
Ochrospora, 349
 Oersted, A. S., 266
Oidia, 126, 299, 300, 309, 313, 314, 316,
 323, 360
Oidiophore, 299
 Olive, Edgar W., 29, 268
Olpidiaceae, 36, 38, 42
Olpidiopsis, 7, 38
 luxurians, 37
 minor, 37
 saprolegniae, 37
Olpidium, 8, 36, 37
 brassicac, 36
 radicale, 38
 viciae, 37
Onygena, 235
Onygenaceae, 231, 234
Oomyceteae, 59, 100
 Oort, A. J. P., 304, 305
Oospora, 126, 383
 lactis, 383
Operculatae, 154
Operculum, 133, 154, 156, 181
Ophiostoma, 189
 Orange, 195, 227
 rust, 257
 Orcein, 6, 128, 152
 Orton, C. R., 204, 268
 Ostiole, 134, 365
Ostropales, 159
Oxalis, 263
 stricta, 267
Oxycoccus macrocarpus, 328
Ozonium, 391
 omnivorum, 392
- P
- Pachyma*, 391
 cocos, 333, 391
Pachyphloeus, 168
Padus, 173

- Palm*, B. T., 34, 89
Palmella, 199
Pampolysporium, 225
Papulospora, 170
 mytilina, 169
 Paragynous antherids, 88
 Paraphyses, 133, 134, 180, 181, 323,
 328
 Parasite, balanced, 4
 destructive, 4
 Paravicini, E., 280
Parmularia, 170, 207
 Parr, Rosalie, 109, 110
 Parthenogenesis, 8, 66
Patella, 157
 scutellata, 158
 Patouillard, N., 297, 310, 312
 Patterson, P. M., 83
Paxillus, 342, 351, 352
 Pea, 194
 Peach, 382
 leaf curl, 173
 Pear, 193, 380
 Pectic compounds, 58
 Pectose, 3, 100, 144
 Peglion, Vittorio, 239
Penicillium, 126, 229, 231, 232, 233,
 383, 384, 386
 commune, 384
 crustaceum, 233
 vermiculatum, 233
Peniophora, 326
Pericystis, 244
 apis, 244
Peridermium, 276
 Peridioles, 363, 364
 Peridium, 25, 35, 261
 Periphyces, 134, 180, 181
 Periplasm, 67, 73, 82, 86, 90, 96
 Perisporiaceae, 218, 219, 224
 Perisporiales, 205, 208, 218
Perisporina manaoensis, 225
Perisporium, 218, 219
 gramineum, 218
 Perithecial appendages, 223
 Perithecium, 134, 179
 structure, 181
Peronosplasmopara, 93
Peronospora, 91, 92, 95, 96
 ficariae, 94
 parasitica, 95
 spinaciae, 95
 Peronosporaceae, 83, 91, 95, 96, 115
 Peronosporales, 8, 58, 59, 60, 77, 82,
 88, 96, 125
Persea, 195
 Persoon, C. H., 13
Pestalotia, 382
 versicolor, 381
Pestalozzia, 382
 Petch, T., 212
 Petersen, H. E., 36
 N. F., 278
 Pethybridge, G. H., 87
 Petrak, F., 204, 205, 213, 375, 377, 378
Peziza, 11, 13, 128, 154, 158, 296, 317
 badia, 158
 venosa, 158
 vesiculosa, 158
 Pezizaceae, 134, 157, 163
 Pezizales, 128, 132, 139, 144, 145, 152,
 161, 166, 167, 173, 182, 208,
 222, 236, 244, 245, 246, 286,
 309, 317, 323, 375, 380, 381,
 385, 391
 Inoperculate forms, 159
 Operculate forms, 157
 Phacidiaceae, 163, 169, 170
 Phacidiales, 160, 206
Phacidium, 163
 lacerum, 163
 Phaeodictyae, 377, 387, 390
 Phaeodidymae, 377, 378, 386
Phaeolus, 336
 Phaeophragmiae, 377, 381, 386, 390
 Phaeosporae, 377, 378, 386, 390
 Phallaceae, 370
 Phalliales, 358, 369, 370, 371
 Phallineae, 372
Phallogaster, 362, 370
Phallus, 5, 11, 12, 13, 370, 371
Phaseolus lunatus, 88, 211
 vulgaris, 268, 325, 391

- Phleogena*, 297, 310, 311, 313, 315
 faginea, 313
Phleogenaceae, 312
Phlyctochytrium, 43
 hallii, 42
Pholiota, 350, 352
 adiposa, 345, 352
 aurivella, 300
 praecox, 345
Phoma, 193, 377, 378, 379
 betae, 194, 378
Phomopsis, 197
Phragmidium, 268, 273, 276
 violaceum, 260
Phragmobasidiaceae, 310
Phragmosporae, 377
Phycomyces, 106, 108
 nitens, 107, 108
Phycomycetaceae, 3, 4, 57, 58, 77, 78, 82,
 124, 125, 236, 240, 243, 244,
 247, 285, 308, 374
Phyllachora graminis, 203
Phyllachoraceae, 203, 204
Phyllactinia, 219, 220, 223, 224
 corylea, 220, 221
Phyllobium, 52, 77
Phyllosticta, 377, 378
 tabifica, 378
Phymatotrichum omnivorum, 385, 392
Physalospora, 194, 378
 cydoniae, 194
Physarum, 24, 27
 nutans, 28
 polycycephalum, 23, 24, 25
Physcia, 150, 151, 184
Physiologic forms, 254, 262
Physiologic races, 254
Physiology of fungi, 7
Physoderma, 48
 maculare, 46, 47, 48
 zeae-maydis, 46, 48
Phytophthora, 86, 88, 91, 95, 96
 cactorum, 88
 erythroseptica, 87
 infestans, 5, 88
 phaseoli, 88
Pichiaceae, 239

Piehl, Addie E., 187
Pierce, Newton B., 172
Pigments, 6
Pilacre, 297, 310
Piline, 225
Pilobolaceae, 109
Pilobolus, 103, 108, 109, 110, 113, 116
 crystallinus, 101
Pinaceae, 273, 275
Pine, 274
Pink mold, 232
Pinus, 274, 275
 strobis, 255, 257, 267
Piptocephalidaceae, 105, 110
Piptocephalis, 108, 110, 113
 freseniana, 101, 106
Piptoporus, 336
Pirus, 193, 380
Pisolithus, 362, 363
Pistillaria, 329
Pisum, 194
Placenta, 204
Plane tree, 195
Plasmodiophora, 34, 35
 brassicae, 31, 32, 33
Plasmodiophorales, 31, 35, 36
Plasmodium, 24, 25, 30
Plasmodiophora, 91, 93
Platanus, 195
Plectania, 158
 coccinea, 158
Plectascales, 135, 180, 228
Plectobasidiales, 361
Plectodiscella veneta, 211
Pleospora, 194, 209, 211, 387
Pleosporaceae, 193, 194, 209, 211
Pleurage, 132, 185, 189, 244
 anserina, 183, 184, 185, 187, 188,
 264, 302
Pleurotus, 350, 352
 ostreatus, 345
 sapidus, 350
 ulmarius, 345
Plowright, C. B., 251, 252
Plum pockets, 173
Pluteus, 352
 cervinus, 345, 352

- Poa*, 224
 pratensis, 282
Poaceae, 92, 224, 284
Podaxineae, 372
Podaxis, 362
Podosphaera, 223, 245
Podospora, 189
Pogonomyces, 338
Poirault, G., 252
Poisonous mushrooms, 347
Poisons, 6
Polyphagus, 44, 45
 euglenae, 44, 45
Polyporaceae, 201, 330, 332, 341, 343,
 344, 351
 sexual reproduction, 333
Polyporus, 9, 12, 333, 336, 337, 338,
 341, 383, 391
 cinnabarinus, 337
 elegans, 336
 sulphureus, 336, 337
Polysphondylium, 30
 violaceum, 29
Polystictus, 334, 337, 341
 abietinus, 338
 perennis, 338
 versicolor, 337
Polystigma, 201
 rubrum, 200
Polystomella, 207
Polystomellaceae, 207
Polythrincium, 386
 trifolii, 386
Poole, R. F., 173
Poplar, 275
Popp, W., 282
Populus, 275
Poria, 335, 337, 341
 albolutescens, 336
Porodaedalea, 338
Porter, C. L., 86
Portulaca oleracea, 91
Potato, 325, 389, 391
Powdery mildews, 219
Primary mycelium, 294, 323
 urediniospore, 271
 zoospore, 69
Primula, dimorphic species, 157
Privileged nuclei, 240, 241
Probasidium, 297, 312
Proliferation of zoosporangia, 69, 71
Promycelium, 129, 252, 256, 297, 319
Protococcus, 199
Protomyces, 119
 inundatus, 120
Protomycetaceae, 119
Protomycetales, 119
Protomycopsis, 119
Prunus, 163, 173, 194, 382, 388
 avium, 173
 cerasus, 173
Psalliota, 308, 350, 353
Pseudolpidiopsis, 37, 38
Pseudo-ostiole, 204, 206
Pseudoparenchyma, 127, 145
Pseudoperonospora, 93, 95
 cellidis, 95
 cubensis, 93
Pseudopeziza, 152, 162
 medicaginis, 162
 ribis, 162, 375, 381
 trifolii, 153
Pseudoplasmodium, 29, 30
Pseudoseptum, 4, 61
Pseudosphaeriaceae, 210
Pseudosphaeriales, 170, 185, 192, 193,
 195, 198, 203, 204, 205, 208,
 209, 211, 213, 378
Pseudosporeae, 50
Pteridophyta, 254, 273
Puccinia, 12, 258, 272, 275, 276
 arenariae, 269
 asparagi, 268
 coronata, 261, 267
 glumarum, 259
 graminis, 16, 258, 261, 262, 263,
 266, 267, 268
 agrostidis, 262
 secalis, 262
 tritici, 4, 254, 262
 helianthi, 261, 263, 264, 267, 268
 malvacearum, 266, 268, 269
 pringsheimiana, 261
 rubigo-vera tritici, 254

- Puccinia, sorghi*, 254, 258, 263, 267
 subnitens, 5
 triticea, 258, 261, 262, 263, 267, 268
Pucciniaceae, 275
Pucciniastrum, 271, 272
Puccinosira, 273
Puff-balls, 365
Pycnidium, 126, 182, 376
Pycniospore, 259
Pycnium, 257
Pycnopus, 337
Pyrenomycetes, 179, 213
Pyrenophora, 211
 terres, 210, 211, 386
 trichostoma, 211
Pyrenula, 199
Pyrenulales, 180, 198
Pyronema, 124, 134, 139, 140, 150, 153, 154, 157, 173, 206, 243
 confluens, 135, 136, 183
 var. *inigneum*, 139
Pyropolyporus, 338, 339
Pythiaceae, 77, 82, 83, 91, 96
Pythiacystis, 88
Pythiomorpha, 89
Pythiopsis, 69, 71
 cymosa, 71
Pythium, 77, 82, 83, 86, 88, 95, 96
 aphanidermatum, 86
 debaryanum, 5, 85
 dictyosporum, 84
 proliferum, 83, 84
 subgenus *Aphragmium*, 85
 Nematosporangium, 85
 Sphaerosporangium, 85
 torulosum, 84
- Q
- Quadripolar sexuality, 304, 305
Quaetia, 369
Quercus, 168, 336, 339
 borealis, 274
 Quince, 194
- R
- Raciborski*, M., 252
Radulum, 331
 Ramlow, G., 153
Ramularia, 385, 386, 388
 tulasnei, 193
Ramularisphaerella, 194
Ranunculaceae, 284, 285
Raspberry, 211
Ravenelia, 273, 276
 Rawitscher, F., 281
Receptive hyphae, 262, 286
Red cedar, 267, 268
Red maple, 164
Red Seaweeds, 140, 144, 247
Reduction division (see also under meiosis), 24, 27
Reed, Geo. M., 224
Reinke, J., 146
Repeating spores, 253
Reproduction of fungi, 7
Respiratory hyphae, 153
Resting sporangia, 61
Reticularia, 24
Rhamnus, 267
Rheosporangium, 86
Rhipidium, 74, 75
 americanum, 74
Rhizidiaceae, 35, 42, 44, 46
Rhizoctonia, 326, 391
 solani, 391
Rhizomorph, 9, 127, 391
Rhizomorpha, 391
 subcorticalis, 391
Rhizomycelium, 45
Rhizophidium, 43, 44, 47
 globosum, 43
Rhizopoda, 77
Rhizopogon, 360, 362, 365
Rhizopogonaceae, 360, 362
Rhizopus, 109
 nigricans, 12, 101, 105
Rhodochytrium, 50, 52
 spilanthidis, 51
Rhodosporae, 349

- Rhysotecta*, 91, 93
australis, 94
viticola, 92, 93
Rhytisma, 163
acerinum, 164
Ribes, 162, 267, 268
nigrum, 268
Rice, Mabel, 255, 262
Rigidiporus, 336
Rogers, Donald P., 318, 324, 326
Rosa, 268
Rose, 268
Rosellinia, 190, 198
necatrix, 190
Rostowzew, S. J., 93
Rubus, 211, 257, 267, 269, 270, 378
Ruhland, W., 295, 309
Russula, 105, 347, 348
Rusts, 4, 89, 126, 129, 246, 251, 253, 254, 285, 286, 297, 300
biological races, 254
control, 268
crosses of, 262
infection by, 257, 265
perennial mycelium, 257
sexual phases, 261
Rye, 202, 267, 268, 278, 284
- S
- Saccardo, P. A., 15, 251, 377, 393
Saccharomyces cerevisiae, 237, 238
ludwigii, 237, 238
Saccharomycetaceae, 236, 237, 239, 241, 247
Saccharomycetales, 7, 9, 124, 132, 133, 139, 140, 141, 218, 235, 236, 239, 243, 244, 245, 246, 247
Saccharum officinarum, 92
Saccobolus, 156
Sagittaria, 279
Salix, 227
Salmon, Ernest S., 224
Salsify, 91
Sammelzelle, 45, 46, 47, 48, 49
Sappin-Trouffy, P., 119, 251
Saprolegnia, 67, 68, 69, 70, 71, 73, 85, 96, 241
monoica var. *glomerata*, 70
parasitica, 7
Saprolegniaceae, 7, 59, 67, 73, 96, 119
Saprolegniales, 3, 8, 39, 52, 57, 58, 59, 60, 66, 77, 78, 82, 83, 86, 88, 96, 119
Sapromyces, 73
Sarcoscypha, 158
Sartoris, George B., 187, 276
Sartory, A., 384
R., 384
Sass, John E., 302
Satina, Sophia, 105
Sawyer, W. H., 118
Scab of apple, 194
of potato, 383
Scale insects, 310
Scheibe, A., 254
Scherffel, A., 50, 77
Schikorra, W., 230, 232
Schizonella, 282
melanogramma, 282
Schizosaccharomyces, 238
octosporus, 237
Schizosaccharomycetaceae, 237, 239
Schneeplia, 207
Schröter, J., 85, 88, 375
Schwartz, E. J., 34, 38
Schweizer, Georg, 153
Scleroderma, 357, 361, 368
Sclerodermataceae, 361, 363, 365
Sclerodermatales, 358, 361
Sclerodermatineae, 372
Sclerospora, 92
graminicola, 92
Sclerotia, 9, 127, 325, 333, 391
Sclerotinia, 9, 134, 152, 161, 391
americana, 6
cinerea, 126
fuckeliana, 140, 385
gladioli, 140, 152, 156, 161, 264
sclerotiorum, 5, 125, 161
Sclerotium, 391
rolfsii, 9

- Scolecosporae, 377, 378, 382, 387
 Scott, C. Emlen, 48
 Seaver, Fred J., 154, 157
Sebacina, 315
Secale, 202
 cereale, 284
 Secondary mycelium, 294, 323
 sporidia, 256
 urediniospores, 271
 zoospores, 69, 70
Secotium, 358, 362
 agaricoides, 362
 erythrocephalum, 361
 Self-sterility, 188
 Senft, E., 125
 Septal perforation, 127
 Septobasidiaceae, 312
Septobasidium, 297, 310, 311, 312, 318,
 319
 atropunctum, 311
Septogloeum, 381
Septonema, 170
 spilomeum, 169
Septoria, 378
 apii, 379
 apii-graveolentis, 379
 lycopersici, 379
 pyricola, 194, 379
Septorisphaerella, 184, 194
 Septum, development, 4
 Serological studies, 286
 Serum diagnosis, 246
Setaria, 92
 Sexual phases, 323
 of Basidiomyceteae, 302
 of Smuts, 280, 281, 284
 reproduction, 7
 strains, 156
 Seyfert, Richard, 276, 277
 Shear, C. L., 188, 211, 264, 313
 Sideris, C. P., 85
Simblum sphaerocephalum, 370
 Siphonaceous algae, 77
 Siphonophyceae, 78
Sirobasidium, 314, 315
 sanguineum, 313
 Skupienski, F. X., 24, 35
 Sleumer, H. O., 277, 280
 Slime Molds, 1, 23
 Smith, Annie L., 152
 Smut galls, 279
 Smuts, 9, 126, 129, 251, 253, 276, 285,
 286
 control of, 278, 279
 genetic studies, 280, 282
 geographic races, 282
 infection by, 278, 281
 monocaryon strains, 281
Solanum tuberosum, 88, 325, 383, 389,
 391
Solenia, 326, 343
Solidago, 275
 Sooty mold, 227
Sordaria, 189
 finicola, 187
 Sordariaceae, 189
 Sorghum, 282
Sorodiscus, 34
 Sorokin, N., 65
Sorosphaera, 34
Sorosporium, 282
 reilianum, 281
 saponariae, 283
 Southworth, E. A., 381
Sparassis, 329, 330
 Sparrow, F. K., 36, 48, 61, 64, 67, 83,
 84, 85
Spathularia, 165, 166
Spegazzinia, 390
 Sperm cells, 259
 distribution, 259, 261
 Spermagonium, 149, 150, 184, 199,
 200, 255, 257, 285, 286
Spermoeidia clavus, 202
Spermophthora, 242, 243, 245, 246
 gossypii, 242
 Sperms, non-motile, 139, 140, 142, 143,
 144, 149
Sphaceloma, 212
Sphacelotheca, 282
 sorgi, 282
 Sphaeriaceae, 190, 192, 198

- Sphaeriales, 139, 144, 152, 170, 180,
185, 198, 199, 200, 202, 203,
204, 205, 206, 208, 209, 210,
211, 213, 219, 229, 244, 246,
375, 378, 381, 386
asexual reproduction, 182
culture of, 187
sexual reproduction, 182
- Sphaerobolaceae, 364, 372
- Sphaerobolus*, 364
grandis, 357
iowensis, 364, 369
stellatus, 364, 369
- Sphaeropsidaceae, 376
- Sphaeropsidales, 170, 376
- Sphaeropsis*, 378
malorum, 194, 378
- Sphaerostilbe*, 201
- Sphaerotheca*, 223, 245
castagnei, 222
fuliginea, 224
mors-uvae, 219
phytophila, 219
- Sphagnum*, 284
- Spilanthes*, 50
- Spinach, 95
- Spinacia oleracea*, 95
- Sponge mushroom, 159
- Spongipellis*, 336
- Spongospora subterranea*, 33, 34
- Sporangiole, 104, 111, 112, 113, 118
- Sporangiophore, 102
- Spore-ball, 34, 280
- Spore cake, 34
- Spore forms, classification by, 377
- Spore-fruit, 8, 124
- Sporidia, 129, 252, 254, 256
discharge of, 256
- Sporodesmium*, 170
- Sporodinia*, 109
grandis, 101, 105, 107
- Sporodochium, 383, 389
- Sporonema*, 195
- Sporophyte, 62
- Sporormia leporina*, 185
- Stakman, E. C., 17, 254, 255, 262, 277,
283
- Staurosporae, 377, 390
- Steinmann, A., 310, 312
- Stem smut, 278
- Stemonitis*, 24, 27
fusca, 23
- Stereum*, 12, 326, 331
- Sterigmata, 323
- Sterigmatocystis*, 232, 384
basidiosepta, 384
- Stevens, F. L., 90, 227
- Stichobasidial nuclear division, 295,
297, 317
- Stigmatea*, 207
robertiani, 206
- Stigmateaceae, 207
- Stigmatomyces baeri*, 142
- Stilbaceae, 383, 388
- Stilbella*, 388
- Stilbum*, 199, 201
- Stinking smut, 278, 284
- Stipe, 349
- Stomatogene*, 225
- Strawberry, 193
- Streaming of cytoplasm, 57
- Strobilomyces*, 342
strobilaceus, 342
- Strobilophyta, 254
- Stroma, 191, 226
- Strömatic Sphaeriales, 195, 196
- Strong, F. C., 110, 158, 159, 160, 164,
202, 337, 346, 347, 363
- Stropharia*, 353
- Stylospore, 113
- Stypella*, 315
- Stysanus*, 389
stemoniles, 388
- Subiculum, 190
- Sugar beet, 388, 391
- Sugar cane, 92
- Suillellus*, 341
luridus, 341
- Suillus*, 12
- Sunflower, 261, 267
- Suspensor, 107
- Swarm-spore, 23, 24, 31
- Sweet potato, 91, 102
- Swingle, D. B., 101

- Sycamore, 195
 Sydow, H., 192, 203, 207, 208, 210,
 219, 227, 271, 375, 377, 378
 Sylloge Fungorum, 15, 393
 Synascus, 120, 245
Syncephalis, 110
 Synchytriaceae, 39, 42
Synchytrium, 8, 39, 52
 endobioticum, 40, 41, 42
 fulgens, 40
 vaccinii, 42
 Synnema, 383, 388
Systemma ulmi, 203
Syzigiles, 109
 Szymanek, Jos., 86
- T
- Taphria*, 173
Taphridium, 119
Taphrina, 140, 172, 173
 alnitorqua, 173
 cerasi, 173
 deformans, 171, 172, 173
 epiphylla, 171
 klebahnii, 171
 potentillae, 173
 pruni, 173
 Taphrinaceae, 171, 173, 309
 Taphrinales, 145, 170, 286, 309, 318
 Targioni-Tozzetti, G., 12
 Tehon, L. R., 387
 Teliospore, 8, 129, 130, 251, 252, 265,
 266, 297, 312
 germination, 252, 266
 Teliosporeae, 129, 251, 285, 286, 297,
 309, 310, 317, 319
 asexual reproduction, 253
 sexual reproduction, 253
 Telium, 260
 forms of, 271
 Terfeziaceae, 231
Tetrachytrium, 66
 triceps, 65
Tetramyxa, 34
Thalictrum, 267
 Thamnidiaceae, 111
Thamnidium, 104, 111, 112
 fresenii, 111
 Thaxter, Roland, 62, 74, 113, 114, 115,
 116, 142, 143, 144
 Theissen, F., 135, 192, 203, 207, 208,
 210, 219, 227
Thelebolus, 244, 245
 stercoreus, 132
Thelephora, 326
 Thelephoraceae, 325, 328, 332, 341,
 343, 351, 358, 391
Thielaviopsis paradoxa, 191
 Thom, Charles, 384
 Thomas, R. C., 125
Thraustotheca, 69, 70
 unisperma, 70
Thuja occidentalis, 345
Tibicina septendecim, 118
Tilletia, 284, 286
 foetens, 5
 levis, 278, 284
 tritici, 5, 278, 284
 Tilletiaceae, 277, 283, 299
 hybridization in, 284
 sexual reproduction, 284
 Tisdale, W. H., 48
Tithymalus, 267
 Toadstool, 347
 Tomato, 239, 379
Tolyposporium, 282
 junci, 283
 Tournefort, Pitton, 11
Trachysphaera, 89
Tragopogon porrifolius, 91
 Trama, 344, 362
 Tramal plates, 360, 362
 tissues, 359
Trametes, 12, 336, 338, 341
 suaveolens, 338
Tremella, 13, 313, 315
 frondosa, 314
 fuciformis, 315
 Tremellaceae, 315
 Tremellales, 129, 297, 310, 313, 315,
 316, 317, 318, 319
Tremellodon, 313, 314, 315
Trentepohlia, 146, 199

- Trichocomaceae, 231
 Trichoglossum, 166
 Trichogyne, 132, 135, 136, 137, 139,
 140, 141, 142, 143, 149, 151,
 152, 163, 179, 180, 184, 246
 in Rusts, 262, 263
 Tricholoma, 347
 equestre, 345
 personatum, 345
 Trichopeltaceae, 207
 Trichophore, 142
 Trichoscyphella, 161
 willkommii, 161
 Trichothecium, 385
 Trichothyriaceae, 228
 Trichothyrium, 228
 Trifolium, 386
 pratense, 153
 Triticum, 202, 224, 267, 282
 aestivum, 254
 durum, 254
 Trophic mycelium, 58
 Trophogone, 137, 187, 229, 230
 Trow, A. H., 83
 Trypethelium, 199
 Tsuga, 339
 Tuber, 10, 12, 167, 168
 aestivum, 168
 brumale, 168
 lapideum, 168, 307
 magnatum, 168
 melanocarpum, 168
 rufum, 168
 Tubera, 10, 11
 Tuberales, 134, 145, 166, 167, 169, 358
 Tubercinia, 277, 285
 trientalis, 283
 Tubercularia, 201, 389
 vulgaris, 389
 Tuberculariaceae, 383, 389
 Tulaane, L. R. and C., 14, 16, 168
 Tulasnella, 318, 319, 326, 327
 anceps, 327
 tulasnei, 324
 Tylopilus, 341
 fellous, 341
 Tylostoma, 296, 368
 campestre, 368
 simulans, 369
 Tylostomataceae, 365, 368, 372
 Typha, 112
 Typhula, 329, 391
- U
- Umbelliferae, 120
 Uncinula, 223, 224
 necator, 219
 Universal veil, 349
 Uredinales, 4, 8, 9, 246, 251, 252, 253,
 254, 279, 281, 285, 286, 299,
 312, 318, 374
 Uredineae, 251
 Uredinal sorus, 265
 Uredinospore, 253, 254, 265
 Uredinium, 260, 265
 forms of, 271
 Uredinopsis, 267, 272, 273
 Uredo, 276, 374
 Uredospore, 253
 Urocystis, 284
 anemones, 284
 occulta, 278, 283, 284
 violae, 284
 Uromyces, 262, 263, 272, 275
 appendiculatus, 261, 268
 caladii, 255
 caryophyllinus, 267
 vignae, 261
 Urophlyctis, 46, 48, 50
 alfalfae, 48, 49
 Ustilaginaceae, 279, 304, 306
 sexual reproduction, 280
 Ustilaginales, 9, 125, 251, 252, 253,
 256, 276, 285, 309, 312, 318,
 374
 asexual reproduction, 277
 Ustilago, 9, 276, 282, 284
 avenae, 278, 281, 282, 295
 hordei, 279, 282
 ischaemi, 281
 levis, 281, 282
 longissima, 281, 306

- Ustilago nuda*, 278, 280, 282
striiformis, 282
tritici, 5, 278, 280, 282
violacea, 279, 281, 282
viijkii, 277
zeae, 277, 278, 279, 280, 281, 282,
 286, 302

V

- Vaccinium*, 273
 Vaillant, Sebastien, 11
Valsa, 197, 198, 378
 Valsaceae, 195
Valsella, 198
 Vandendries, René, 17, 299, 300, 301,
 304, 305
 Varitchak, Bogdan, 187, 241, 244, 245
Vaucheria, 68, 77, 78
 Vaucheriaceae, 78
Venturia inaequalis, 184, 186, 194, 385
Verpa, 159
Verrucaria, 198
 Vesicle, 84
 Vincens, F., 182, 190
Viola, 284
odorata, 387
 Violet, 387
Vitis, 190, 193, 219
vinifera, 193
 Vizioli, J., 191
Volutella, 389
dianthi, 389
 Volva, 349
Volvaria, 344, 352
 Voss, W., 254
 Vuillemin, Paul, 297, 309

W

- Wager, H., 45
 Waite, M. B., 173
 Walker, Leva B., 113, 114, 241, 364
 Wartenweiler, Alfred, 95
 Waterhouse, W. L., 262, 267
 Weber, G. F., 112

- Wehmeyer, Lewis E., 182, 190, 195,
 196
 Welsford, E. J., 200
 von Wettstein, Fritz, 33, 39, 58, 59,
 100, 125
 Wheat, 202, 254, 267, 268, 278, 282,
 284
 Whetzel, H. H., 385
 White Pine, 257, 267
 Blister Rust, 255, 267, 268
 Rust, 89
 Wieben, Magdalene, 171
 Wilcox, Marguerite S., 188
 Williamson, H. S., 137, 139
 Willow, 227
 Wilson, Guy West, 91
 Malcolm, 24
 O. T., 50
 Witches' Broom, 257, 273
 Wolf, Frederick A., 112, 328
 Wood-inhabiting fungi, 294, 332
 Woronin, M. S., 16, 283, 327
Woronina, 38
polycystis, 38
 Woroninaceae, 36, 38, 50, 52, 77

X

- Xylaria*, 187, 198
hypoxylon, 198
polymorpha, 198
subterranea, 191
 Xylariaceae, 190, 195, 197, 198, 201

Y

- Yeasts, 132, 236, 237, 245
 Young, Elaine M., 230, 232

Z

- Zaghouania*, 256
 Zahlbruckner, A., 152
Zea mays, 92, 267, 282, 390
 Zeller, A. M., 359
 Zender, Justin, 238, 239
 Ziegenspeck, H., 133, 285

Zodiomyces, 143
 vorticellarius, 141, 142
Zoosporangium, 58
Zoospore, 35, 58, 119, 125
Zopf, Wilhelm, 76, 129
Zygnematales, 119
Zygochytrium, 66, 119
 aurantiacum, 65
Zygomyceteae, 59, 100, 119

Zygomycetes, 251
Zygorhynchus, 108
Zygosaccharomyces, 7, 238
 chevalieri, 238
 pastorii, 238
Zygosaccharomycetaceae, 237
Zygospore, 8, 59, 102, 105, 107
Zythia, 379
Zythiaceae, 379

